PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
116(3):661–691. 2003.

Redescription of adults and description of copepodid development of *Dermatomyzon nigripes* (Brady & Robertson, 1876) and of *Asterocheres lilljeborgi* Boeck, 1859 (Copepoda: Siphonostomatoida: Asterocheridae)

V. N. Ivanenko and Frank D. Ferrari

(VNI) Department of Invertebrate Zoology, Biology Faculty, Moscow State University, Moscow 119 899, Russia;
(FDF) Department of Systematic Biology, National Museum of Natural History, Smithsonian Institution, Museum Support Center, 4210 Silver Hill Rd., Suitland, Maryland 20746, U.S.A.

Abstract.—Adult and immature copepodids of *Dermatomyzon nigripes* (Brady & Robertson, 1876) and *Asterocheres lilljeborgi* Boeck, 1859 were collected by SCUBA from the White Sea. All copepodids of *D. nigripes* were found on the bryozoan *Flustra foliacea* (Linnaeus, 1758); adults of *D. nigripes* also were washed out from the sponge *Halichondria panicea* (Pallas, 1766), the ophiuroid *Ophiopholis aculeata* (Linnaeus, 1767), and were collected among hydrozoans and other invertebrates from dead shells swept by tidal currents. Copepodids of *A. lilljeborgi* were washed from the starfish *Henricia sanguinolenta* (O. F. Müller, 1776). Comparative analysis of development of *D. nigripes* and *A. lilljeborgi* with the related *Scottomyzon gibberum* (Scott & Scott, 1894) shows that both genders of *A. lilljeborgi* and *S. gibberum* suppress the formation of fourth abdominal somite. Females of *A. lilljeborgi* and *D. nigripes* develop a simple segmental complex when the arthrodial membrane separating the genital somite from the second abdominal somite fails to form; this arthrodial membrane develops on females of *S. gibberum* so that there is no genital complex. The antennule of *A. lilljeborgi* with a single, proximal complex of three segments appears most similar to the ancestral siphonostomatoid. The antennule of *D. nigripes* has a proximal complex of two segments and a distal complex of three segments; the antennule of *S. gibberum* has a proximal complex of three segments and a distal complex of four segments. Setation of the maxilliped of *D. nigripes* and *A. lilljeborgi* are identical and appear similar to the ancestral siphonostomatoid; the maxilliped of *S. gibberum* differs in that it fails to add a seta to its syncoxa and loses a seta on the penultimate endopodal segment. *Asterocheres lilljeborgi* and *S. gibberum* share derived states of setation on the exopod of swimming legs 1–4, leg 5 and leg 6; *D. nigripes* and *S. gibberum* share derived states of setation on the endopod of swimming legs 3 and 4.

Copepods belonging to the family Asterocheridae Giesbrecht 1899 have been collected as free-living from the benthopelagic zone, or from benthic samples taken in association with cnidarians, echinoderms, sponges, ascidians and bryozoans from all oceans of the world. Forty of 45 genera of asterocherids have been described from shallow marine waters, and five from deep waters. Four of the five deep water genera are found in galls of corals (Stock 1981, 1984); the monotypic genus *Cheramomyzon* Humes, 1989 is found in deep water seeps off Florida. In addition, one species of the shallow water genus *Collocherides* Canu, 1893 has been collected from a deep water hydrothermal vent in the northeast Pacific Ocean (Humes 1999). The family Asterocheridae and the deep water hydrothermal vent family Dirivultidae Humes & Dojiri, 1980 share character states often considered ancestral for the order Siphonostomatoida in phylogenetic analyses of copepod orders (Ho 1990, Huys & Boxshall 1991, Martínez Arbizu 2003). Detailed descriptions of development of asterocherid species are essential in analyzing the ancestral states, transformations, and homologies of characters of that order and of the subclass Copepoda. Ivanenko et al. (2001) provide the only description of development of a siphonostomatoid, *Scottomyzon gibberum* (Scott & Scott, 1894), associated with an invertebrate, the starfish *Asterias rubens* Linnaeus, 1758. *Scottomyzon gibberum* previously was included in Asterocheridae, but was placed in Scottomyzontidae by Ivanenko et al. (2001). In the present paper, adults are redescribed and all juvenile copepodid stages are described of *Dermatomyzon nigripes* (Brady & Robertson, 1876) and *Asterocheres lilljeborgi* Boeck, 1859, both collected from the White Sea. *Dermatomyzon nigripes* is the only species of the genus. *Asterocheres lilljeborgi* is the oldest of 60 nominal species in its genus, and taxonomic studies of the genus have been published continuously since its discovery.

Methods

All measurements and dissections were made for copepodids from the Karelian coast of the Gulf of Kandalaksha, White Sea, near the Marine Station of Moscow State University, 66°31′N, 33°07′W. Benthic invertebrates were collected individually in plastic bags during SCUBA dives from 5–25 m. About five volumes of fresh water were added to one volume of the seawater in the plastic bag with invertebrates for 30 min. The bag was agitated and the water passed through a 20 micron mesh net. Copepodids conforming to stages I–VI were recovered from these net samples and fixed with 70% ethanol; no nauplii were collected. Copepodids were cleared in lactic acid following the method of Humes & Gooding (1964), and stained by adding a solution of chlorazol black E dissolved in 70% ethanol/30% freshwater (Ferrari 1995). Drawings were made with a camera lucida.

The first to sixth copepodid stages are CI–CVI. Thoracic somites are abbreviated Th; abdominal somites are Abd. CR is the caudal ramus. Somites are numbered according to their relative developmental age following Hulsemann (1991); thoracic somites and abdominal somites, except the most posterior anal somite, increase in age and decrease in numeral designation anteriorly. The anal somite bearing the caudal rami is designated as the first abdominal somite because developmentally it is the oldest abdominal somite. The first thoracic somite bears the maxilliped; the genital openings are found on the seventh thoracic somite.

The number of segments of the antennule often are difficult to determine because the arthrodial membrane separating segments may be very thin and difficult to observe; armament of an antennular segment is given as "setae + aesthetascs". Although patterning of copepod swimming legs during development are only incompletely known, the model of proximal patterning (Ferrari & Benforado 1998) is followed here. Ramal segments of swimming legs 1–4 (thoracopods 2–5) are referred to by their presentation during development (Ferrari 1995). The terms "seta" and "spine" are used for articulating cuticular elements connected by an arthrodial membrane to an appendage segment; setae appear to be less rigid than spines. In order to maintain continuity among descriptive publications, tables of setae and spines on swimming legs 1–4 in the descriptive section follow the formula introduced by Lang (1934). In the formula, Roman numerals indicate spines and Arabic numerals are setae. Numerals to the left of a comma or dash indicate lateral elements; numerals between two commas are terminal elements, and numerals to the right of a comma or dash are medial elements. A semicolon separates ramal segments and an asterisk indicates that the segment is absent. It should be noted, however, that this kind of formula is not derived from the way a swimming leg is patterned during development, in which the distal arthrodial membrane of a segment is formed one copepodid stage later than the formation of the initial seta of the segment (Ferrari & Benforado 1998). Thus, setal and segmental homologies cannot be determined correctly from the formula. Setules are epicuticular extensions of a seta; denticles are epicuticular extensions of an appendage segment; spinules are epicuticular extensions of a somite. Only authors who have contributed descriptions and/or illustrations are cited in the synonymy section.

Dermatomyzon nigripes (Brady & Robertson, 1876)
Figs. 1–8

Dermatomyzon nigripes Brady and Robertson, 1876.—Giesbrecht, 1899:77–78, pl. 1, fig. 4, pl. 5, figs. 1–14.—Sars, 1914: 95–97, pls. 59, 60.—Lang, 1949:5, fig. 8.—Eiselt, 1965:155–158, fig. 3A–J.—Boxshall, 1990:537–539, figs. 9–11.—Gotto, 1993:166, figs. 40P–Q, 41A–D.

Dermatomyzon giesbrechti Brady, 1910: 574–577, textfigure 60, pl. 58, fig. 11.

Dermatomyzon nigripes giesbrechti Brady, 1910.—Eiselt, 1965:155.

Dermatomyzon elegans Claus, 1889:351, pl. 6.

Dermatomyzon herdmani Brady, 1910:575, fig. 61.

Cyclopicera nigripes Brady & Robertson, 1876:197.—Brady, 1880:54–56, pl. 89, figs. 1–11.—Thompson, 1893:36, pl. 25, fig. 7.

Ascomyzon thorelli Sars, 1880:474–75.

CVI female (Fig. 1A, B).—Body length range 1.20–1.36 mm (based on 3 specimens); average length of prosome 0.84 mm; maximum width of prosome 0.62 mm; length of urosome 0.46 mm; length of genital complex 0.15 mm; width of genital complex 0.17; ratio of length to width of prosome 1.4; ratio of length of prosome to length of urosome 1.8.

Prosome (Fig. 1A, B): 4 articulating sections; 1st a complex of 5 cephalic somites plus Th1, 2; Th3–5 articulating.

Urosome (Fig. 1C, D): 5 articulating sections; Th6, genital complex of Th7 fused to Abd2 [an unsclerotized area separates anterior neck from remaining part of Th7], Abd3, 4, 1 articulating. On genital complex, paired copulatory pores ventral-lateral to oviducal openings; paired oviducal openings dorsal.

Egg sacs spherical with up to 8 eggs (Fig. 1F).

Rostrum (Fig. 1B): Pointed in lateral view.

Oral cone (Fig. 1E): Beak-like.

Antennule (Fig. 1G, H): 19 articulating segments with 1, 2, 4, 2, 2, 2, 2, 6, 1, 2, 2, 2, 2, 2, 2, 2, 2+1, 1, 11.

Antenna (Fig. 1I): Coxa and basis without setae; basis with denticle. Exopod 1-segmented with 1 terminal seta and 1 proximal seta. Endopod 2-segmented; 1st segment with denticles; 2nd segment with denticles and 5 setae, largest thick and with curved tip.

Mandible (Fig. 1J): Gnathobase 2× length of palp, tapering and slightly curved distally with denticles; 1-segmented palp with denticles and 2 terminal setae.

Maxillule (Fig. 1K): Inner lobe bearing several series of denticles and armed with 5 setae; outer lobe articulating proximally, with 1 short and 2 long setae terminally and 1 long subterminal seta.

Maxilla (Fig. 2C): Apparently 2-segmented subchela; 1st segment with proximal asthetasc; 2nd segment curved and pointed distally with indistinct arthrodial membranes at distal 3rd and distal 6th of

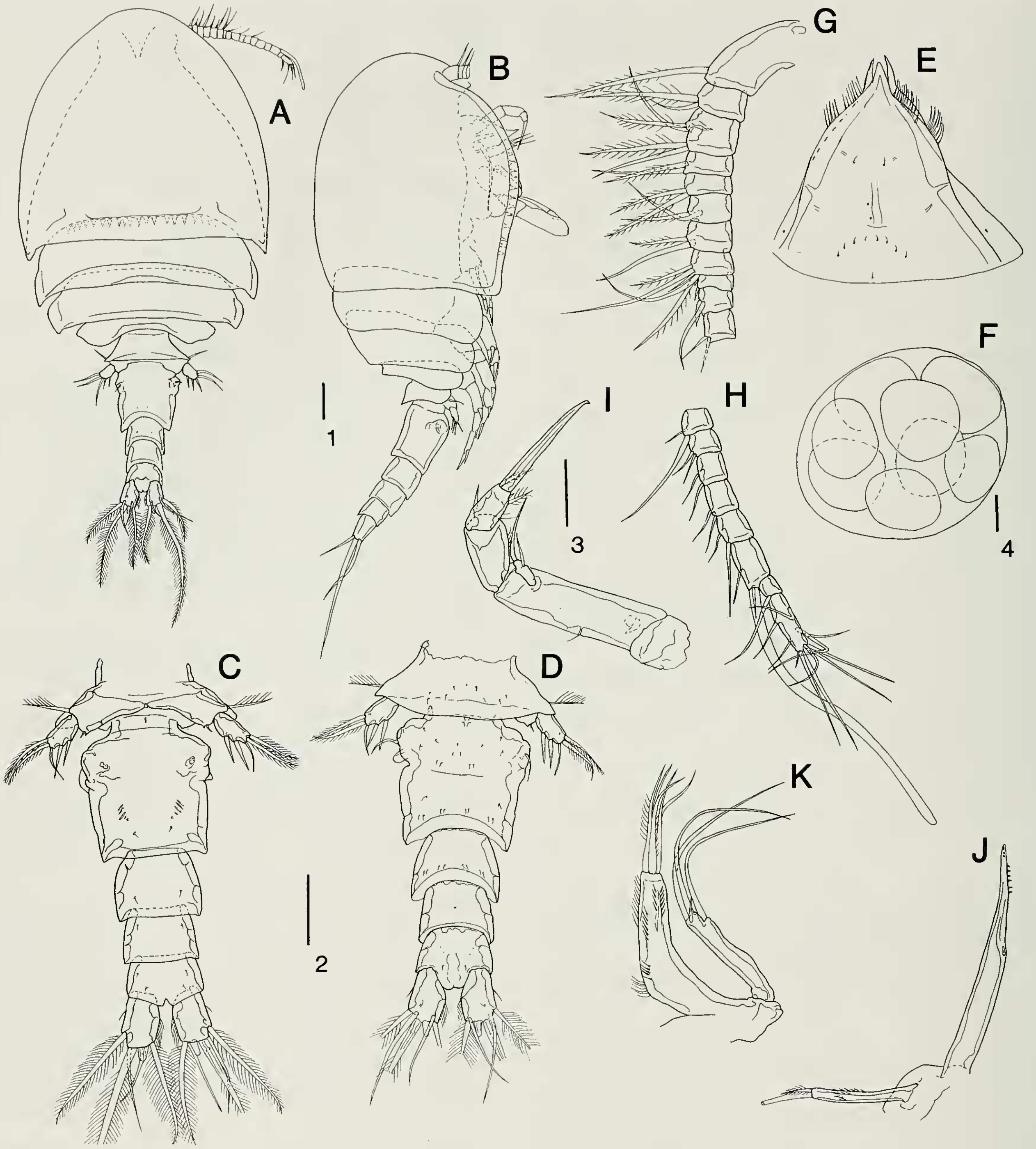

Fig. 1. *Dermatomyzon nigripes* (Brady & Robertson, 1876), CVI Female: A, habitus, dorsal; B, habitus, lateral; C, urosome, ventral; D, urosome, dorsal; E, labrum, anterior; F, eggs; G, antennule, segments 1–11; H, antennule, segments 12–19; I, antenna; J, mandible; K, maxillule. Scale line 1 is 0.1 mm for A, B; line 2 is 0.1 mm for C, D; line 3 is 0.1 mm for E, G–K; line 4 is 0.1 mm for F.

its length, with small, inner seta and several sets of denticles.

Maxilliped (Fig. 2A, B): Short, syncoxa with 1 inner seta, long basis with 1 inner seta on medial margin; endopod of proximal, short, apparently subdivided section with 1 medially and 2 distally polarized setae, and distal segment with 2 terminal setae, largest thick and claw-like.

Swimming legs 1–4 (Fig. 2D–G): Biramal, with 3-segmented rami; all with intercoxal sclerite and 2-segmented protopods. Formula for spines and setae (Table 1). Distal exopodal seta adjacent to terminal spine of swimming legs 3–4 very small.

Leg 5 (Fig. 2I): Basis not articulating with somite and bearing medial denticle and lateral seta; exopod elongate with 1 thin

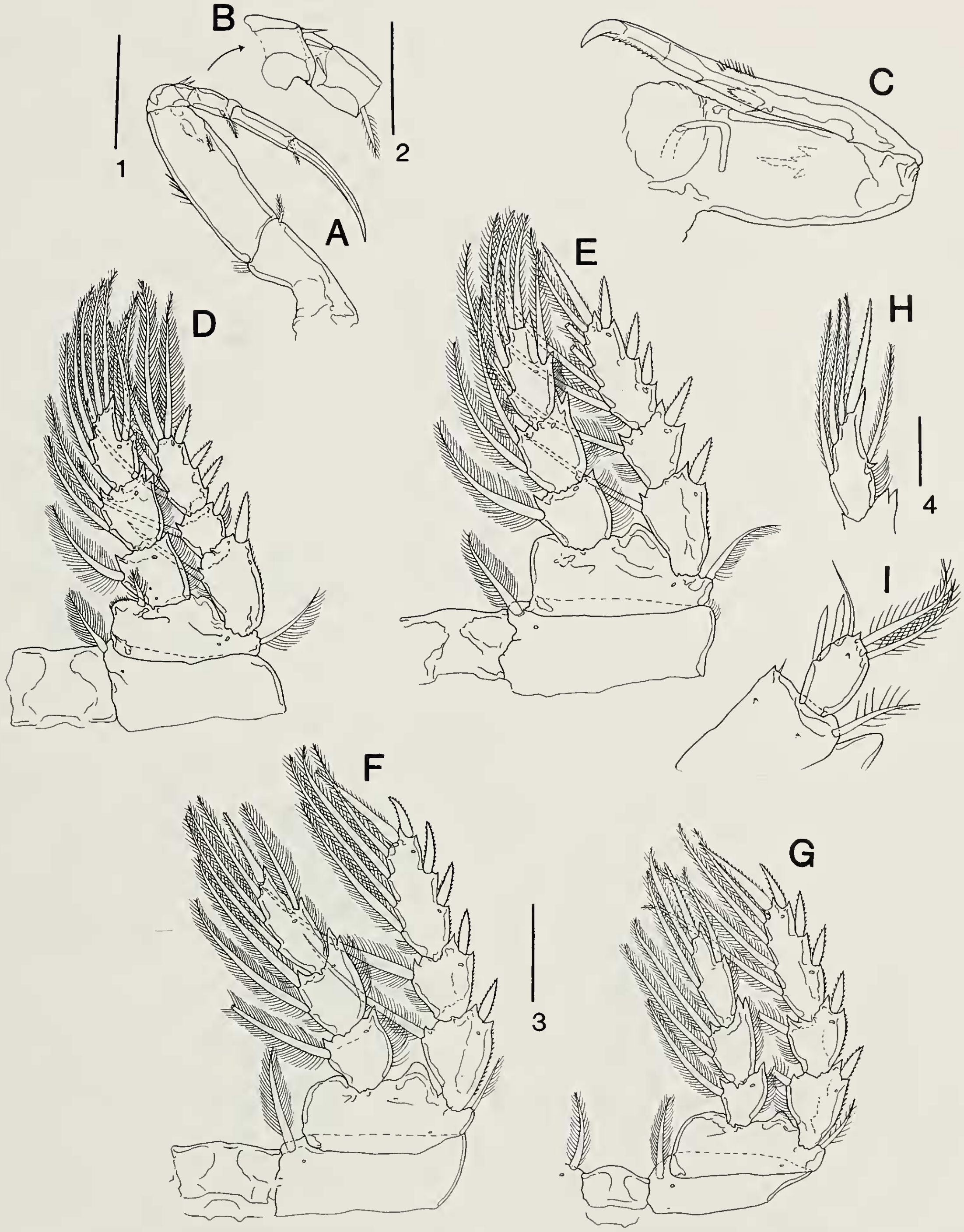

Fig. 2. *Dermatomyzon nigripes* (Brady & Robertson, 1876), CVI Female: A, maxilliped; B, proximal part of endopod of maxilliped, posterior; C, maxilla; D, swimming leg 1; E, swimming leg 2; F, swimming leg 3; G, swimming leg 4; I, leg 5. *Dermatomyzon nigripes* CVI male: H, swimming leg 3, distal segment of endopod. Scale line 1 is 0.1 mm for A; line 2 is 0.05 mm for B; line 3 is 0.1 mm for C–G; line 4 is 0.05 mm for H, I.

Table 1.—Spines and setae on swimming legs 1–4 of *Dermatomyzon nigripes* CVI female.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0–1	1–1	I-1; I-1; III, 1, 4	0–1; 0–2; 1, 2, 3
Leg 2	0–1	1–0	I-1; I-1; III, I, 5	0–1; 0–2; 1, 2, 3
Leg 3	0–1	1–0	I-1; I-1; III, I, 5	0–1; 0–2; 1, I, 3
Leg 4	0–1	1–0	I-1; I-1; III, I, 5	0–1; 0–2; 1, I, 2

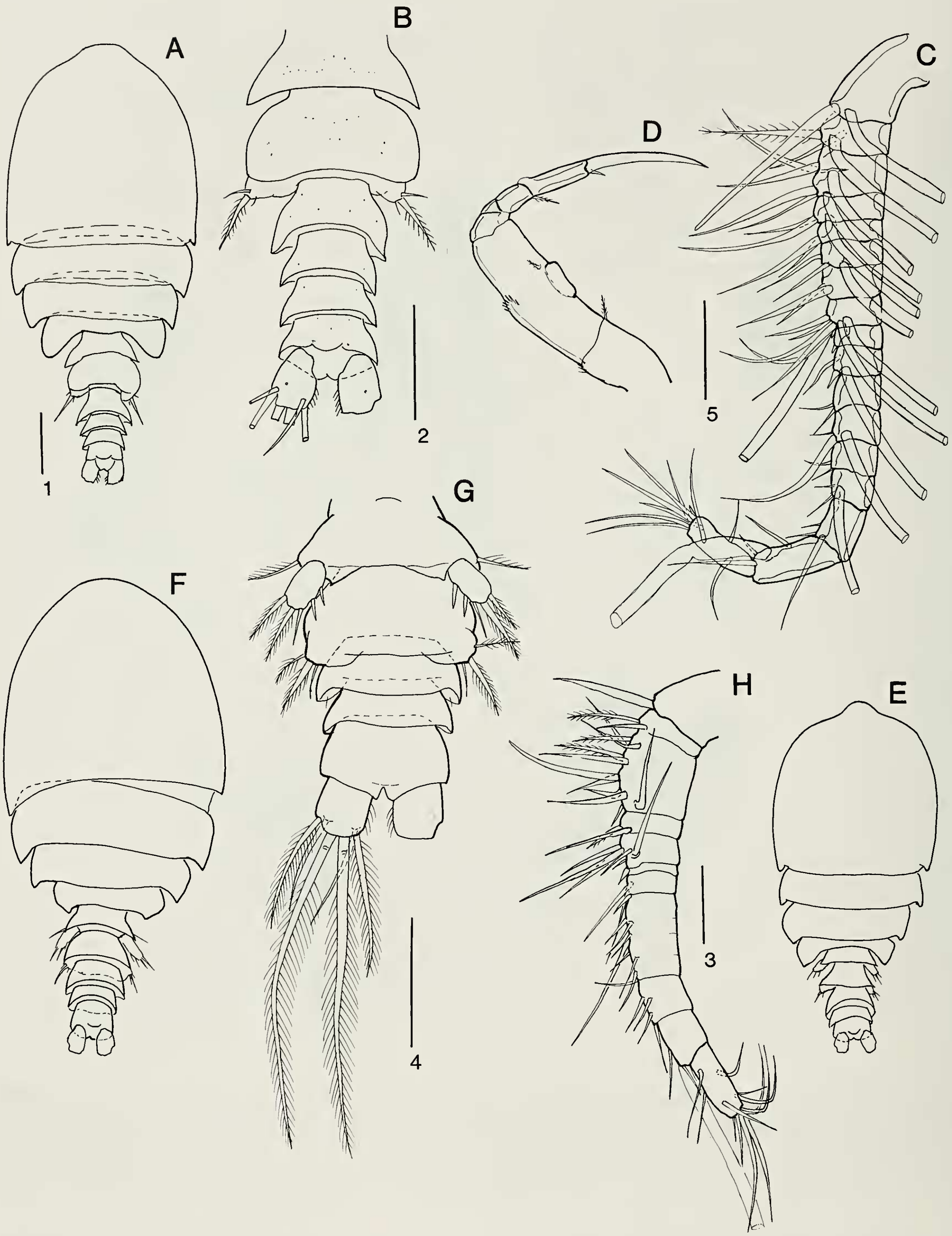

Fig. 3. *Dermatomyzon nigripes* (Brady & Robertson, 1876), CVI Male: A, habitus, dorsal; B, urosome, dorsal; C, antennule; D, maxilliped. *Dermatomyzon nigripes* CV Male: E, habitus, dorsal. *Dermatomyzon nigripes* CV Female: F, habitus, dorsal; G, urosome, ventral; H, antennule. Scale line 1 is 0.1 mm for A, E, F; line 2 is 0.1 mm for B; line 3 is 0.1 mm for H; line 4 is 0.1 mm for D, G; line 5 is 0.1 mm for C.

and 2 thick unarmed setae laterally and 2 longer setae with setules medially.

Leg 6 (Fig. 1D): 1 long, thin seta and 2 very small setae near oviducal opening.

CR (Fig. 1C, D): Subquadrate with denticles and 1 lateral, dorsal seta, 1 medial dorsal seta, and 4 terminal setae.

CVI male (Fig. 3A).—Differs from CVI female as follows: Body length range 0.90–1.08 mm (based on 3 specimens); average length of prosome 0.59 mm; maximum width of prosome 0.42 mm; length of urosome 0.33 mm; ratio of length to width of prosome 1.4; ratio of length of prosome to length of urosome 1.8.

Urosome (Fig. 3B): 6 somites; Th7 articulating with Abd2; copulatory pore ventrolateral.

Antennule (Fig. 3C): 17 articulating segments with: 1+1, 2+1, 4+2, 2+1, 2, 2+1, 2, 6+3, 1, 2+1, 2, 2+1, 2, 2+1, 3, 3+1, 10. Geniculation between articulating segments 16 and 17; articulating segments 14–17 arc-like with articulating segment 15 flexed ventrally toward segment 14 and articulating segment 16 flexed ventrally toward segment 15.

Maxilliped (Fig. 3D): Basis with raised pad-like section proximally and medially.

Swimming leg 3 (Fig. 2H): Tip of lateral seta of distal endopodal segment not reaching to apex of terminal spine; segmental attenuation proximal to lateral seta points medially, not distally.

Leg 6 (Fig. 3B): 3 distolateral setae.

CV female (Fig. 3F).—Differs from CVI female as follows: Body length range 0.98–1.00 mm (based on 2 specimens); average length of prosome 0.67 mm; maximum width of prosome 0.47 mm; length of urosome 0.32 mm; ratio of length to width of prosome 1.4; ratio of length of prosome to length of urosome 2.1.

Urosome (Fig. 3G): 5 articulating sections; Th6, 7, Abd1–3 articulating. Th7 without copulatory pores or oviducal openings.

Antennule (Fig. 3H): 11 articulating segments with 1, 2, 11, 2, 6, 1, 3, 8, 4, 2+1, 12.

Leg 6 (Fig. 3G): 3 distolateral setae.

CV male (Fig. 3E).—Differs from CV female as follows: Body length range 0.73–0.74 mm (based on 2 specimens); average length of prosome 0.49 mm; maximum width of prosome 0.33 mm; length of urosome 0.25 mm; ratio of length to width of prosome 1.5; ratio of length of prosome to length of urosome 2.0.

Antennule: 11 articulating segments with 1, 2, 10, 2, 6, 1, 3, 8, 4, 2+1, 12.

CIV (Fig. 4A).—Differs from CV female as follows: Body length range 0.65–0.72 mm (based on 2 specimens); average length of prosome 0.48 mm; maximum width of prosome 0.32 mm; length of urosome 0.21 mm; ratio of length to width of prosome 1.5; ratio of length of prosome to length of urosome 2.3.

Urosome (Fig. 4B): 4 articulating sections; Th6, 7, Abd2, 1 articulating.

Antennule (Fig. 4C): 9 articulating segments with 1, 6, 1, 5, 2, 8, 4, 2+1, 12.

Antenna (Fig. 4D), maxillule (Fig. 4E) and maxilliped (Fig. 4F, G): As illustrated.

Swimming legs 1–4 (Figs. 4H, I; 5A, B): Small, distal seta adjacent to terminal spine of the exopod of swimming legs 3–4. Formula for spines and setae (Table 2).

Leg 5 (Fig. 4B): Basis not articulating with somite and bearing lateral seta; exopod elongate with 1 thin, unarmed seta medially, 1 thick, unarmed seta laterally and 1 terminal seta with setules.

Leg 6 (Fig. 4B): 2 distal setae.

CIII.—Differs from CIV female as follows: Body length 0.51 mm (based on 1 specimen); length of prosome 0.36 mm; maximum width of prosome 0.26 mm; length of urosome 0.15 mm; ratio of length to width of prosome 1.4; ratio of length of prosome to length of urosome 2.4.

Urosome (Fig. 5C, D): Th6, 7, Abd1 articulating.

Antennule (Fig. 5G): 8 articulating segments with 2, 3, 4, 1, 4, 2, 2+1, 11.

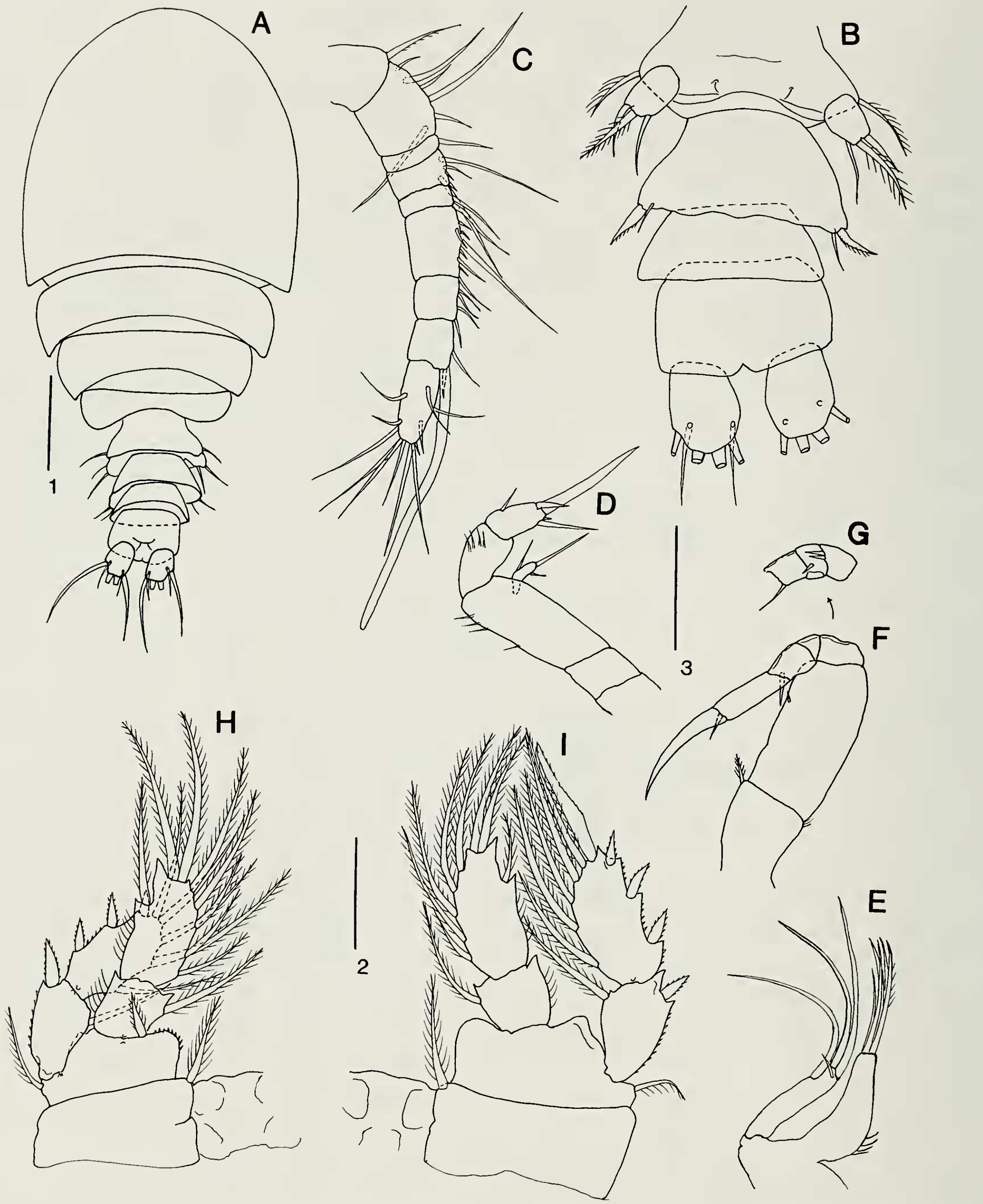

Fig. 4. *Dermatomyzon nigripes* (Brady & Robertson, 1876), CIV Female: A, habitus, dorsal; B, urosome, ventral; C, antennule; D, antenna; E, maxillule; F, maxilliped; G, maxilliped, proximal part of endopod, posterior; H, swimming leg 1; I, swimming leg 2. Scale line 1 is 0.1 mm for A; line 2 is 0.05 mm for B, C, H, I; line 3 is 0.05 mm for D–G.

Antenna (Fig. 6B) and mandible (Fig. 6A): As illustrated.

Maxillule (Fig. 6C): Outer lobe with 3 setae; inner lobe with 4 setae.

Maxilla (Fig. 6D): 3-segmented with indistinct arthrodial membrane distally.

Maxilliped (Fig. 6E): Proximally, endopod indistinctly segmented with 1 seta.

Swimming legs 1–4 (Fig. 6F–I): Swimming legs 1–3 with 2-segmented rami, swimming leg 4 with 1-segmented rami. Distal exopodal seta adjacent to terminal

Table 2.—Spines and setae on swimming legs 1–4 of *Dermatomyzon nigripes* CIV female.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0–I	1–1	I-1; *; III, 5	0–1; *; 1, 2, 5
Leg 2	0–1	1–0	I-1; *; III, 1, 5	0–1; *; 1, 2, 5
Leg 3	0–1	1–0	I-1; *; III, I, 5	0–1; *; 1, I, 4
Leg 4	0–1	1–0	I-0; *; III, I, 5	0–1; *; 1, I, 3

spine of swimming legs 3, 4 tiny. Formula for setae and spines (Table 3).

Leg 5 (Fig. 5E): A unilobe ventrolateral bud with 1 distal spine and 1 distal seta.

CR (Fig. 5F): As illustrated.

CII.—Differs from CIII as follows: Body length 0.4 mm (based on 1 specimen); length of prosome 0.29 mm; maximum width of prosome 0.19 mm; length of urosome 0.13 mm; ratio of length to width of prosome 1.5; ratio of length of prosome to length of urosome 2.2.

Prosome (Fig. 7A, B): 3 articulating sections; 1st complex of 5 cephalic somites plus Th1, 2; Th3, 4 articulating.

Urosome (Fig. 7A, B): Th5, 6, Abd1 articulating.

Antennule (Fig. 7D): 6 articulating segments with 2, 3, 3, 1, 1+1, 11.

Antenna (Fig. 7E), mandible (Fig. 7H) and maxilla (Fig. 7F): As illustrated.

Maxillule (Fig. 7I): Inner lobe with 3 setae.

Maxilliped (Fig. 7G): Syncoxa without seta, basis without seta; proximal section of endopod with 1 distally polarized seta and 1 medial seta; distal segment with 2 terminal setae, 1 claw-like.

Swimming legs 1–3 (Fig. 7K–M): Swimming legs 1–2 with 2-segmented rami, swimming leg 3 with 1-segmented rami. Tiny distal seta adjacent to terminal spine of the exopod of swimming leg 3. Formula for spines and setae (Table 4).

Swimming leg 4 (Fig. 7C): A ventrolateral, bilobe bud; dorsal lobe with 1 distal spine and 1 distal seta; ventral lobe unarmed.

CR (Fig. 7J): As illustrated.

CI.—Differs from CII as follows based on 1 specimen: length 0.36 mm; maximum width 0.16 mm; length of prosome 0.22 mm, urosome 0.14 mm; ratio of length to width 2.25:1; ratio of length of prosome to that of urosome 1.65:1.

Prosome (Fig. 8A, B): 2 articulating sections; 1st, complex of 5 cephalic somites plus Th1, 2; Th3 articulating.

Urosome (Fig. 8A, B): Th4, 5, Abd1 articulating.

Antennule (Fig. 8E): 4 articulating segments with 2, 2, 1, 11+1.

Antenna (Fig. 8F), mandible (Fig. 8G), maxillule (Fig. 8H) and maxilla (Fig. 8I): As illustrated.

Maxilliped (Fig. 8L): Syncoxa and basis unarmed. Endopod of 2 distinct segments; proximal segment with 1 medial seta and distal segment with 2 setae.

Swimming legs 1–2 (Fig. 8J, K): 1-segmented rami. Formula for spines and setae (Table 5).

Swimming leg 3 (Fig. 8C): Ventrolateral, bilobe bud; dorsal lobe with 1 distal spine and 1 distal seta; ventral lobe unarmed.

CR (Fig. 8D): Inner terminal seta longest; remaining terminal setae decreasing in length from inner to outer.

Remarks.—The monotypic genera *Dermatomyzon* Claus, 1889, *Australomyzon* Nicholls, 1944, and *Cheramomyzon* Humes, 1989 share appendage segmentation and segmental armature with species of *Rhynchomyzon* Giesbrecht, 1895. Females of *Dermatomyzon* with a 19-segmented antennule differ from females of *Australomyzon* with a 21-segmented antennule. Females of *Dermatomyzon* differ from females of the poorly-diagnosed *Rhynchomyzon* with antennules of between 14 and 16 segments, by the well-developed rostrum or by the posterolateral extensions of thoracomeres 3 and 4. The mandibular palp of *Cheramomyzon* is 2-segmented but 1-segmented in *Dermatomyzon.* The fifth leg of *Australomyzon* is 1-segmented but 2-segmented in *Dermatomyzon. Dermatomyzon*

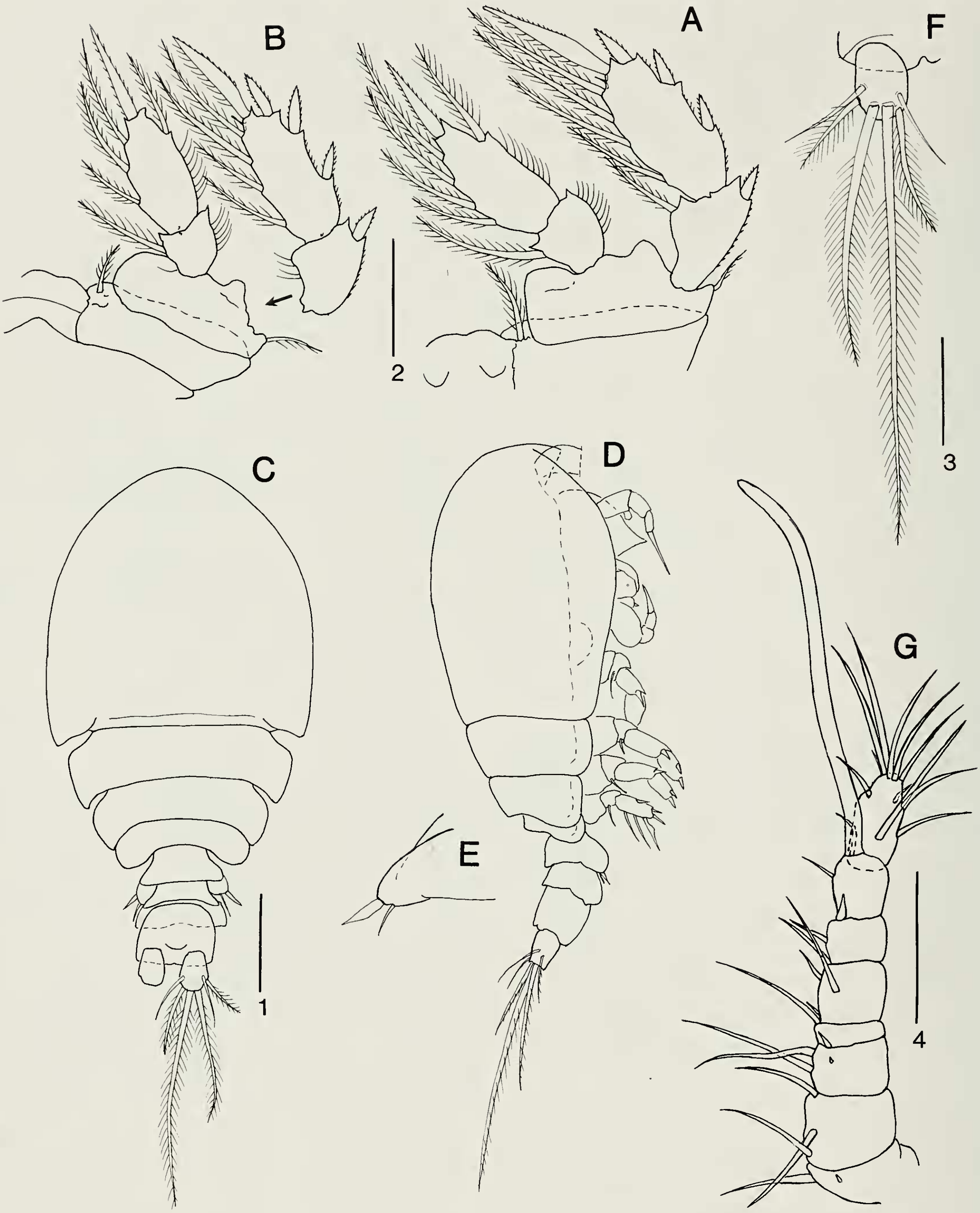

Fig. 5. *Dermatomyzon nigripes* (Brady & Robertson, 1876), CIV Female: A, swimming leg 3; B, swimming leg 4. *Dermatomyzon nigripes* CIII: C, habitus, dorsal; D, habitus, lateral; E, leg 5; F, caudal ramus, dorsal; G, antennule. Scale line 1 is 0.1 mm for C, D; line 2 is 0.05 mm for A, B; line 3 is 0.05 mm for E–F; line 4 is 0.05 mm for G.

nigripes initially was described from the North Sea coast of England. Subsequently it has been reported from areas adjacent to the North Sea (Hansen 1923, Stephensen 1929, Jespersen 1940, Lang 1949), the Mediterranean Sea (Giesbrecht 1899), the Arctic Ocean (Shih et al. 1971), the Indian Ocean (Sewell 1949, Ummerkutty 1966), the Pacific Ocean (Boxshall 1990), and the Southern Ocean (Brady 1910). In the White Sea, copepodids of *D. nigripes* were found on the bryozoan *Flustra foliacea* (Linnaeus,

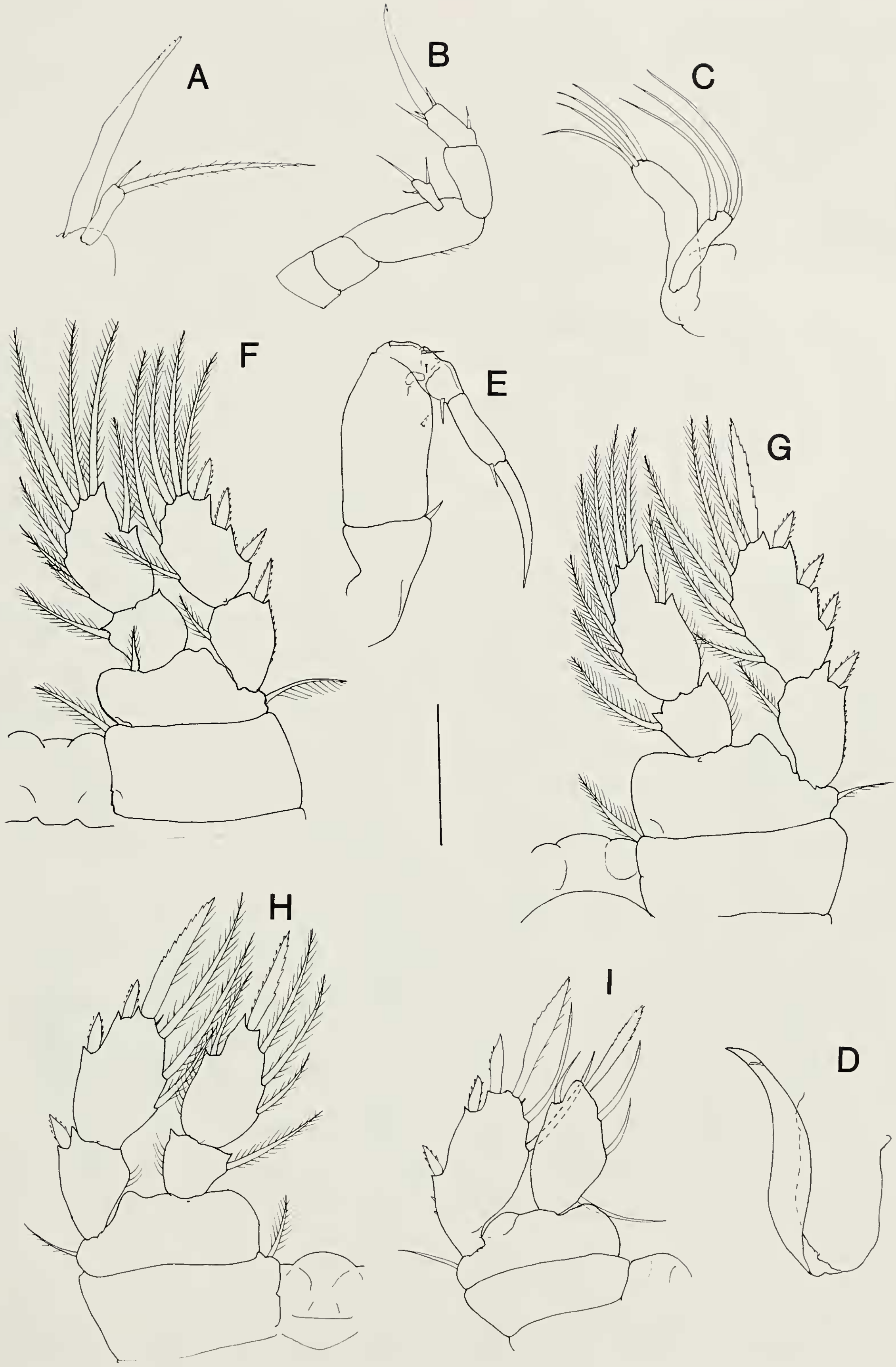

Fig. 6. *Dermatomyzon nigripes* (Brady & Robertson, 1876), CIII: A, mandible; B, antenna; C, maxillule; D, maxilla; E, maxilliped; F, swimming leg 1; G, swimming leg 2; H, swimming leg 3; I, swimming leg 4. Scale line is 0.05 mm.

Table 3.—Spines and setae on swimming legs 1–4 of *Dermatomyzon nigripes* CIII.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0–1	1–1	I-1; *; III, 4	0–1; *; 1, 2, 5
Leg 2	0–1	1–0	I-1; *; III, I, 5	0–1; *; 1, 2, 4
Leg 3	0–1	1–0	I-0; *; II, I, 4	0–1; *; 1, I, 3
Leg 4	0–0	1–0	*; *; III, I, 3	*; *; I, I, 3

Table 4.—Spines and setae on swimming legs 1–3 of *Dermatomyzon nigripes* CII.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0–1	1–1	I-0; *; III, 5	0–1; *; 1, 2, 4
Leg 2	0–1	1–0	I-0; *; II, I, 4	0–1; *; 1, 2, 3
Leg 3	0–0	1–0	*; *; III, I, 3	*; *; 1, I, 3

1758). A small number of adults of *D. nigripes* were washed from the sponge *Halichondria panicea* (Pallas, 1766) and the echinoderm *Ophiopholis aculeata* (Linnaeus, 1767). Adults also were collected around hydrozoans and other invertebrates from bottom covered by dead shells scoured by strong tidal currents. These findings suggest that adults of *D. nigripes* may be an unspecialized symbiont associated with different invertebrates of the White Sea sublittoral. However, immature copepodids of *D. nigripes,* along with other copepods, were associated only with *Flustra foliacea* (see Ivanenko & Smurov 1997) suggesting that the bryozoan may be the preferred host of the immature copepodids.

Asterocheres lilljeborgi Boeck, 1859
Figs. 9–18

Asterocheres lilljeborgi Boeck, 1859:176, pl. 2, figs. 1–11.—Brady, 1880:64–65.—Canu, 1892:264, pl. 27, figs. 1–6.—Giesbrecht, 1899:70, 73, pl. 3, figs. 21–26.—Wilson, 1944:547, pl. 30, figs. 161–162.—Roettger et al. 1972:259, figs. 1–9.—Gotto, 1993:153, fig. 36 B–J.

Ascomyzon asterocheres Sars, 1914:85–87, pls. 51–52.

CVI female.—Body length range 1.41–1.47 mm (based on 3 specimens); average length of prosome 0.99 mm; maximum width of prosome 1.09 mm; length of urosome 0.44 mm; length of genital complex 0.16 mm; width of genital complex 0.21; ratio of length to width of prosome 0.9; ratio of length of prosome to length of urosome 2.3.

Prosome (Fig. 9A): Flattened dorsoventrally with tergites pointed posteriorly; 4 articulating sections; 1st complex of 5 cephalic somites plus Th1, 2 with spinules; Th3–5 articulating.

Urosome (Fig. 9B): 4 articulating sections; Th6, genital complex of Th7 fused to Abd2, Abd3, and Abd1. Th6 and genital complex with spinules; paired copulatory pores ventrolateral; paired oviducal openings dorsolateral.

Rostral area flattened; rostrum absent.

Oral siphon (Fig. 10D): Tip reaching beyond base of maxilla.

Labrum: With spinules on tip.

Antennule (Fig. 9E, F): 21 articulating segments with 2, 2, 2, 2, 2, 2, 2, 2, 6, 2, 2, 2, 2, 2, 2, 2, 2, 2+1, 2, 2, 8.

Antenna (Fig. 10A): Coxa and basis without setae. Exopod apparently 1-segmented with 2 terminal setae and proximal medial seta (Fig. 10B). Endopod 3-segmented; 1st segment with denticles, 2nd with 1 seta, 3rd with denticles and 4 setae, including large terminal claw.

Mandible (Fig. 10C): Gnathobase slightly longer than palp, tapering distally with denticles; 2-segmented palp, both segments with denticles, distal segment with 2 terminal setae.

Maxillule (Fig. 10E): Inner lobe with several sets of denticles, 4 large setae and 1 small seta; outer articulating lobe with denticles and 4 terminal setae.

Maxilla (Fig. 10F): An apparently 2-segmented subchela; 1st segment unarmed; 2nd segment distally pointed, curved, with set of denticles but without setae.

Maxilliped (Fig. 10G, H): Short syncoxa

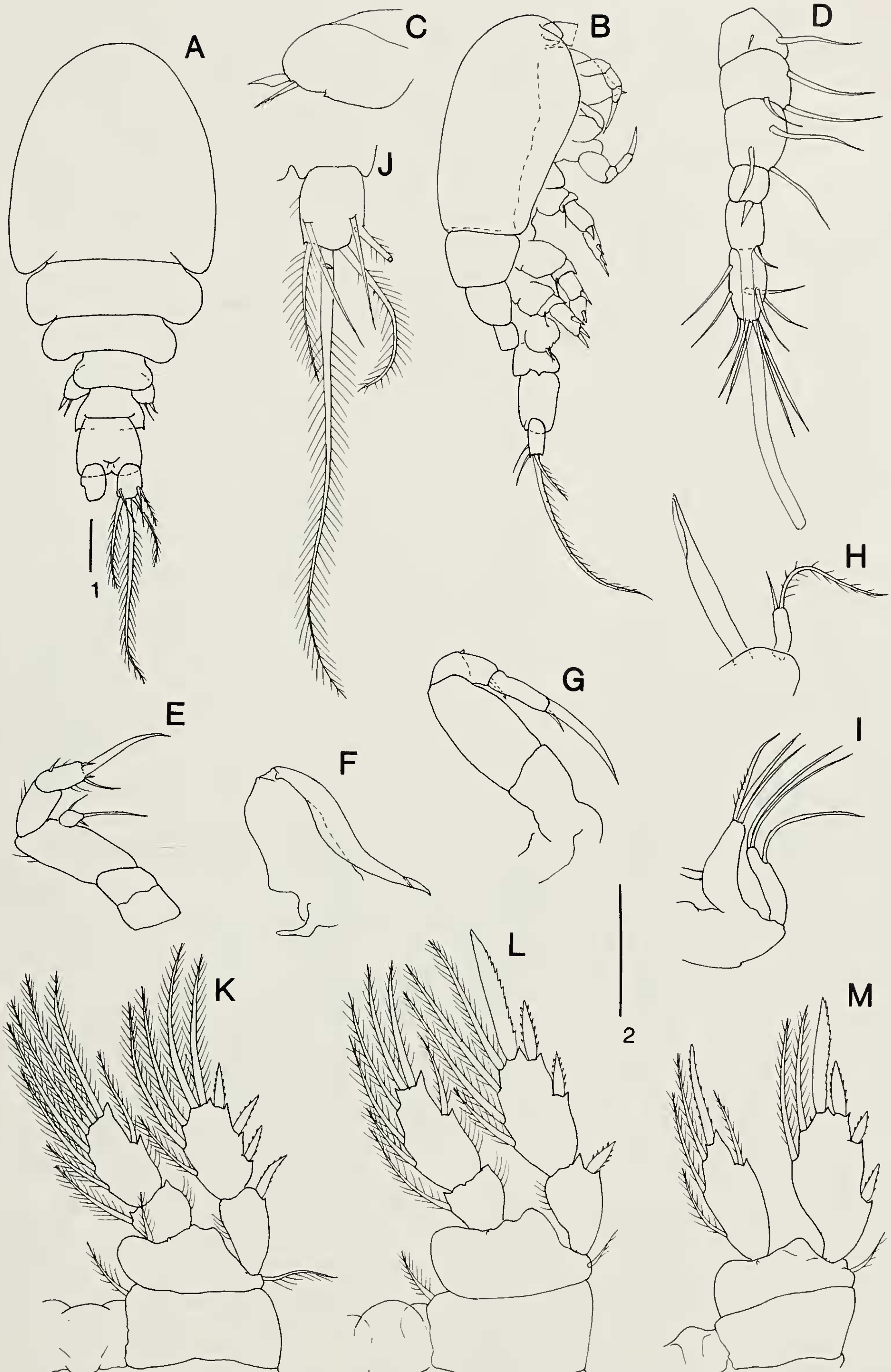

Fig. 7. *Dermatomyzon nigripes* (Brady & Robertson, 1876), CII: A, habitus, dorsal; B, habitus, lateral; C, swimming leg 3; D, antennule; E, antenna; F, maxilla; G, maxilliped; H, mandible; I, maxillule; J, caudal ramus; K, swimming leg 1; L, swimming leg 2; M, swimming leg 3. Scale line 1 is 0.05 mm for A, B; line 2 is 0.05 mm for C–M.

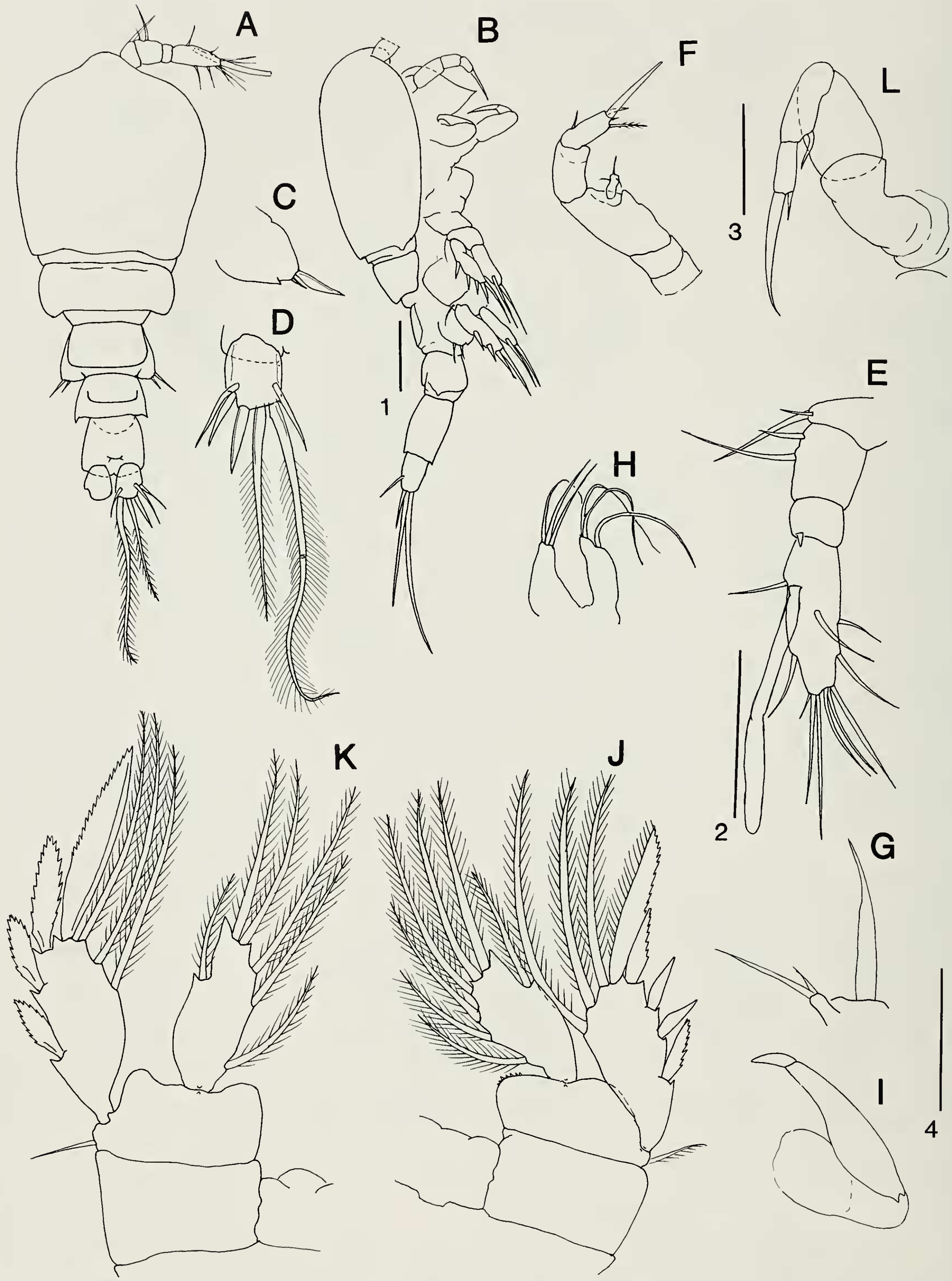

Fig. 8. *Dermatomyzon nigripes* (Brady & Robertson, 1876), CI: A, habitus, dorsal; B, habitus, lateral; C, swimming leg 3; D, caudal ramus; E, antennule; F, antenna; G, mandible; H, maxillule; I, maxilla; J, swimming leg 1; K, swimming leg 2; L, maxilliped. Scale line 1 is 0.05 mm for A, B; line 2 is 0.05 mm for C–E, J, K; line 3 is 0.05 mm for F, H, L; line 4 is 0.05 mm for G, I.

Table 5.—Spines and setae on swimming legs 1–2 of *Dermatomyzon nigripes* CI.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0–0	1–0	*; *; IV, I, 3	*; *; 1, 2, 4
Leg 2	0–0	1–0	*; *; III, I, 3	*; *; 1, 2, 3

with 1 inner seta, long basis with 1 tiny, inner seta on medial margin; endopod of proximal, short, apparently subdivided section with 4 setae, 2 proximal, 1 middle, 1 distal; long distal segment with denticles and 2 terminal setae, largest thick and curved.

Swimming legs 1–4 (Fig. 11A–E): Biramal, with 3-segmented rami. Formula for spines and setae (Table 6). Lateral seta of the distal endopodal segment of swimming leg 3 not reaching tip of lateral apical seta; lateral apical seta of the distal endopodal segment of swimming leg 4 half the length of apical spine.

Leg 5 (Fig. 11F): Basis not articulating with somite, with lateral seta; articulating segment elongate with 2 unarmed terminal setae and 1 medial seta, plus medial and lateral denticles.

Leg 6 (Fig. 9C): 1 long seta and 1 short seta near oviducal openings.

CR (Fig. 9D): Subquadrate with 2 dorsal setae and 4 terminal setae.

CVI male.—Differs from CVI female as follows: Body length range 1.01–1.06 mm (based on 3 specimens); average length of prosome 0.70 mm; maximum width of prosome 0.70 mm; length of urosome 0.36 mm; ratio of length to width of prosome 1.0; ratio of length of prosome to length of urosome 1.9.

Urosome (Fig. 12A): Th6, 7, Abd2, 3, 1 articulating. Th7 with copulatory pore ventrolaterally.

Antennule (Fig. 12B–D): 18 articulating segments with: 2, 2, 2, 2, 2, 2, 2, 2, 6, 2, 2, 2, 2, 2, 2, 4, 3+1, 12. Geniculation between 15th and 16th articulating segments; segment 10 unsclerotized dorsally.

Maxilla (Fig. 12G): Apparently 3-segmented subchela; 1st segment with proximal denticles; 2nd with 1 small seta; 3rd distally pointed and curved.

Maxilliped (Fig. 12H): Basis with raised bump proximally and medially.

Swimming legs 1–4 (Fig. 11G–J): Swimming leg 1 with denticles on distal segment of endopod. Distal attenuation of middle segment of endopod of swimming leg 2 relatively longer than corresponding structure on other swimming legs; denticles on distal segment of endopod. Lateral seta on distal endopodal segment of swimming leg 3 almost reaching to tip of apical seta. Lateral apical seta on distal endopodal segment of swimming leg 4 reaching ¾ length of apical spine.

Leg 5 (Fig. 12F): As illustrated.

Leg 6 (Fig. 12E): Several sets of denticles and 2 setae, distal thickest.

CV female (Fig. 13A).—Differs from CVI female as follows: Body length range 0.84–1.05 mm (based on 7 specimens); average length of prosome 0.64 mm; maximum width of prosome 0.62 mm; length of urosome 0.30 mm; ratio of length to width of prosome 1.0; ratio of length of prosome to length of urosome 2.1.

Urosome (Fig. 13A): Th6, 7, Abd2, 3,1 articulating; no copulatory pore or oviducal openings on Th7.

Antennule (Fig. 13C): 18 articulating segments with 2, 2, 2, 2, 2, 2, 2, 2, 8, 2, 2, 4, 2, 2, 2, 2, 2+1, 14.

Leg 6 (Fig. 13A): Uniramal bud with 1 lateral seta and medial denticles.

CV male (Fig. 13B).—Differs from CV female as follows: Body length range 0.85–0.89 mm (based on 2 specimens); average length of prosome 0.59 mm; maximum width of prosome 0.54 mm; length of urosome 0.29 mm; ratio of length to width of prosome 1.1; ratio of length of prosome to length of urosome 2.5.

Leg 6: Unilobe bud with 1 lateral seta and 1 terminal seta.

CIV.—Differs from CV female as follows: Body length range 0.65–0.80 mm (based on 7 specimens); average length of

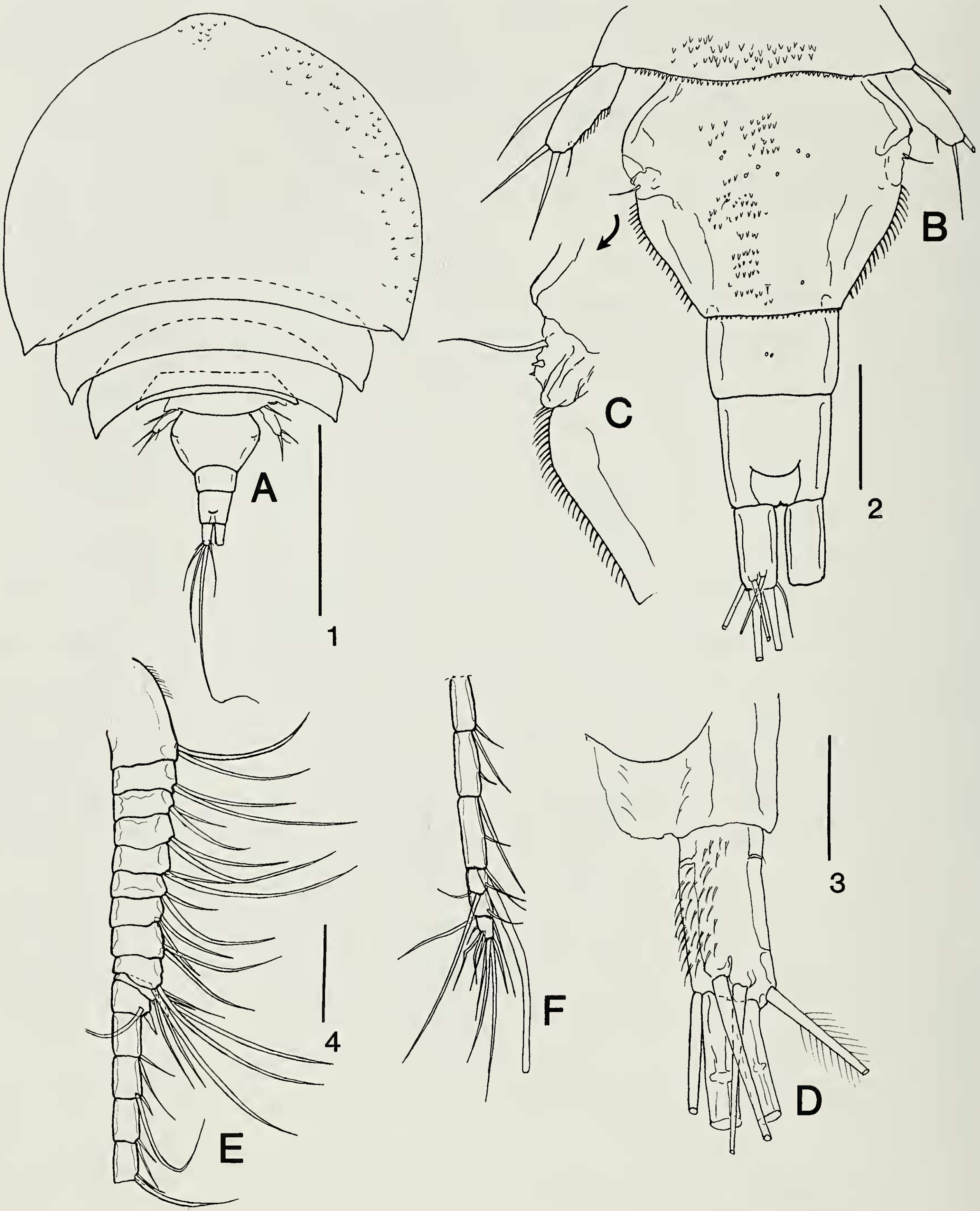

Fig. 9. *Asterocheres lilljeborgi* Boeck, 1859, CVI: A, Female, habitus, dorsal; B, urosome, dorsal; C, leg 6; D, caudal ramus, dorsal; E, antennule, segments 1–15; F, antennule, segments 16–21. Scale line 1 is 0.1 mm for A; line 2 is 0.1 mm for B; line 3 is 0.1 mm for C, D; line 4 is 0.1 mm for E, F.

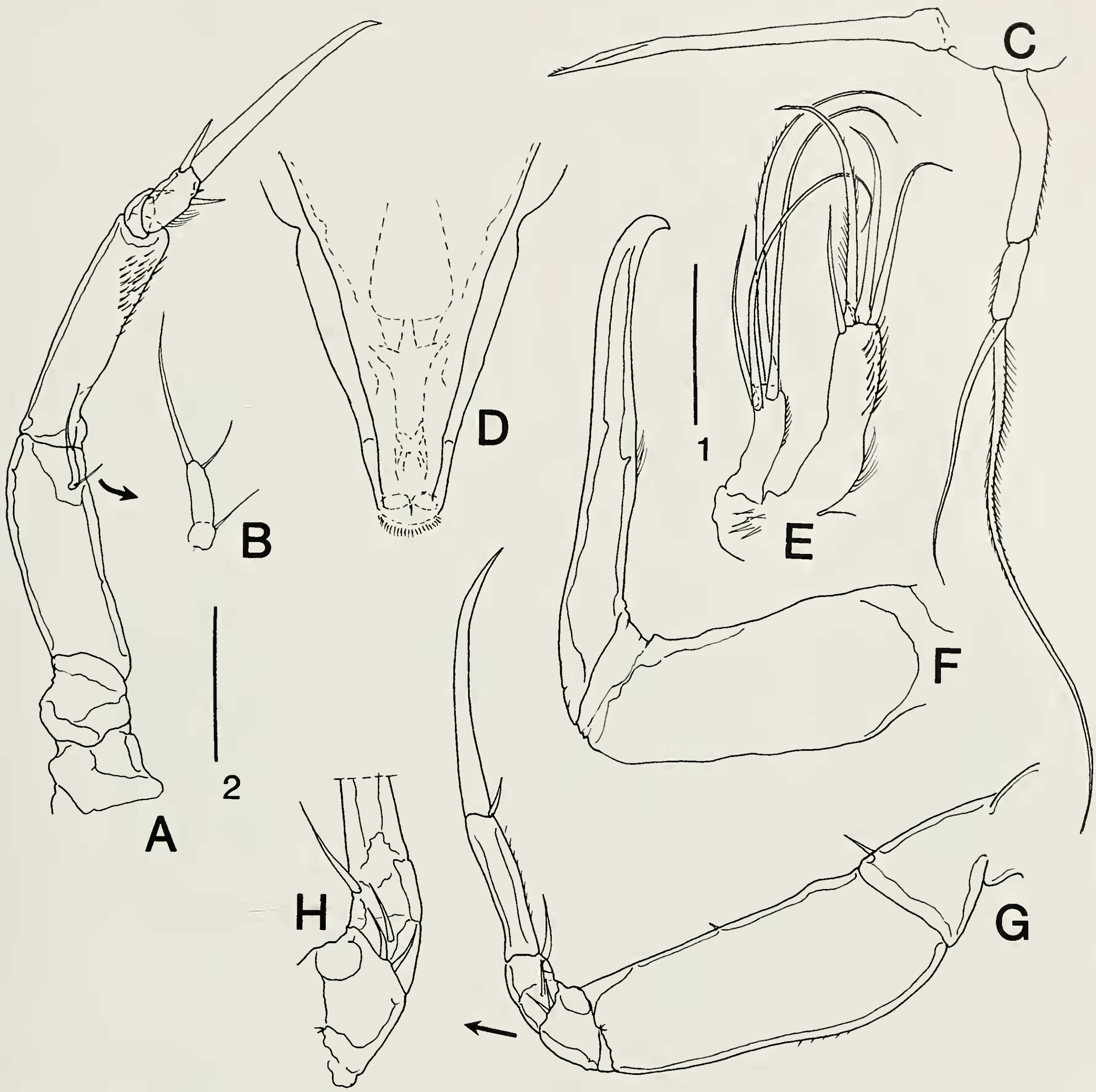

Fig. 10. *Asterocheres lilljeborgi* Boeck, 1859, CVI Female: A, antenna; B, exopod of antenna; C, mandible; D, oral siphon; E, maxillule; F, maxilla; G, maxilliped; H, proximal part of endopod of maxilliped, posterior. Scale line 1 is 0.1 mm for A, C–G; line 2 is 0.05 mm for B, H.

prosome 0.48 mm; maximum width of prosome 0.40 mm; length of urosome 0.22 mm; ratio of length to width of prosome 1.2; ratio of length of prosome to length of urosome 2.2 (Fig. 13E).

Urosome (Fig. 13G): Th6, 7, Abd2, 1 articulating.

Antennule (Fig. 13F): 17 articulating segments with 2, 1, 1, 1, 1, 1, 1, 1, 4, 1, 2, 4, 4, 2, 2, 2+1, 14.

Maxilla as illustrated (Fig. 14A).

Swimming legs 1–4 (Figs. 14B–F): 2-segmented rami. Formula for spines and setae (Table 7).

Leg 5 (Fig. 13G): Basis not articulating with somite, with lateral seta; free segment with 1 small seta laterally and 2 thick, unarmed setae distally.

Leg 6 (Fig. 13G): Unilobe bud with 1 seta.

CIII.—Differs from CIV as follows: Body length range 0.50–0.54 mm (based on 3 specimens); average length of prosome 0.37 mm; maximum width of prosome 0.30

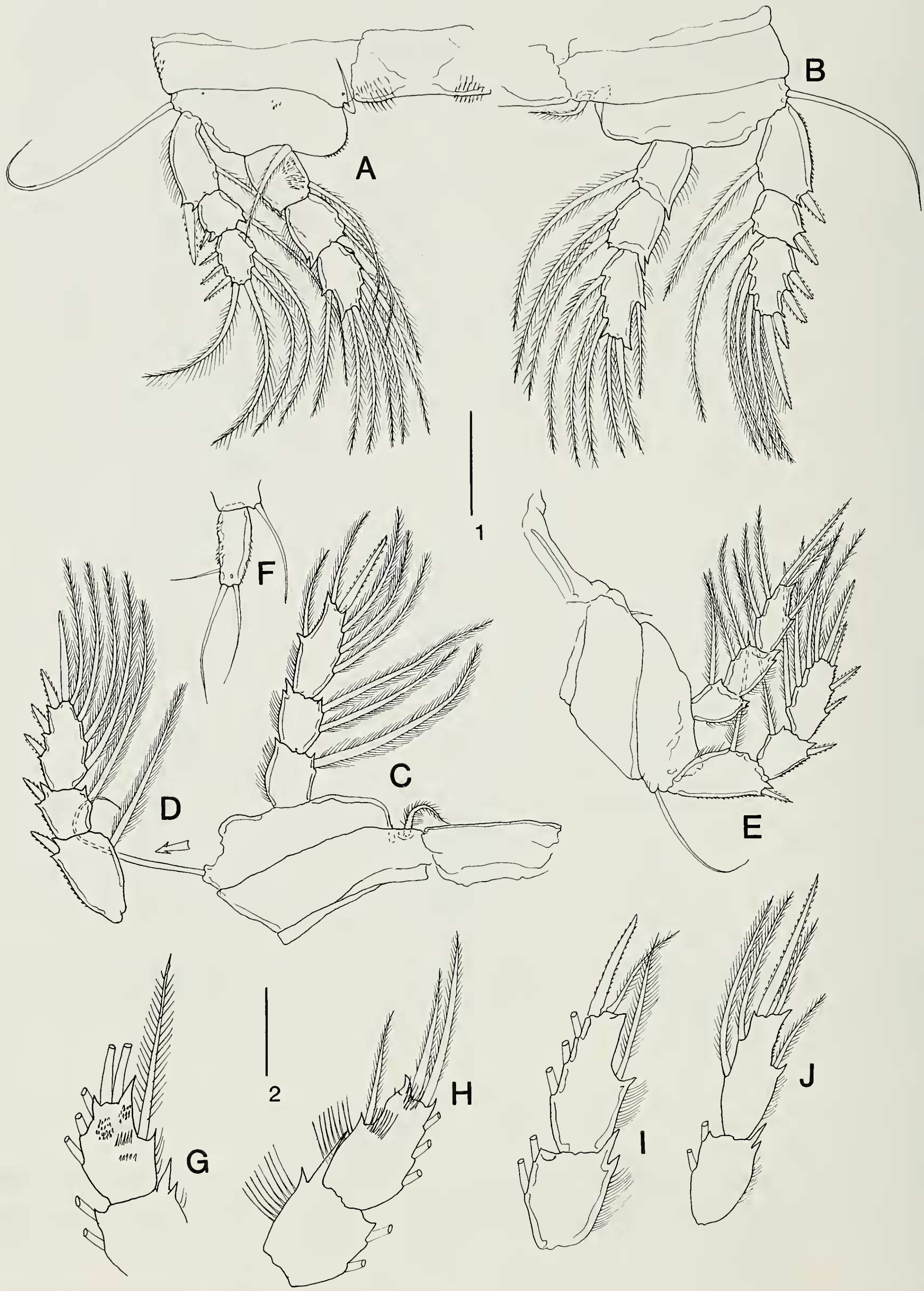

Fig. 11. *Asterocheres lilljeborgi* Boeck, 1859, CVI Female: A, swimming leg 1; B, swimming leg 2; C, intercoxal sclerite, protopod, and endopod of swimming leg 3; D, exopod, swimming leg 3; E, swimming leg 4; F, leg 5. *Asterocheres lilljeborgi,* CVI Male, distal segments of endopod of G, swimming leg 1; H, swimming leg 2; I, swimming leg 3; J, swimming leg 4. Scale line 1 is 0.1 mm for A–F; line 2 is 0.1 mm for G–J.

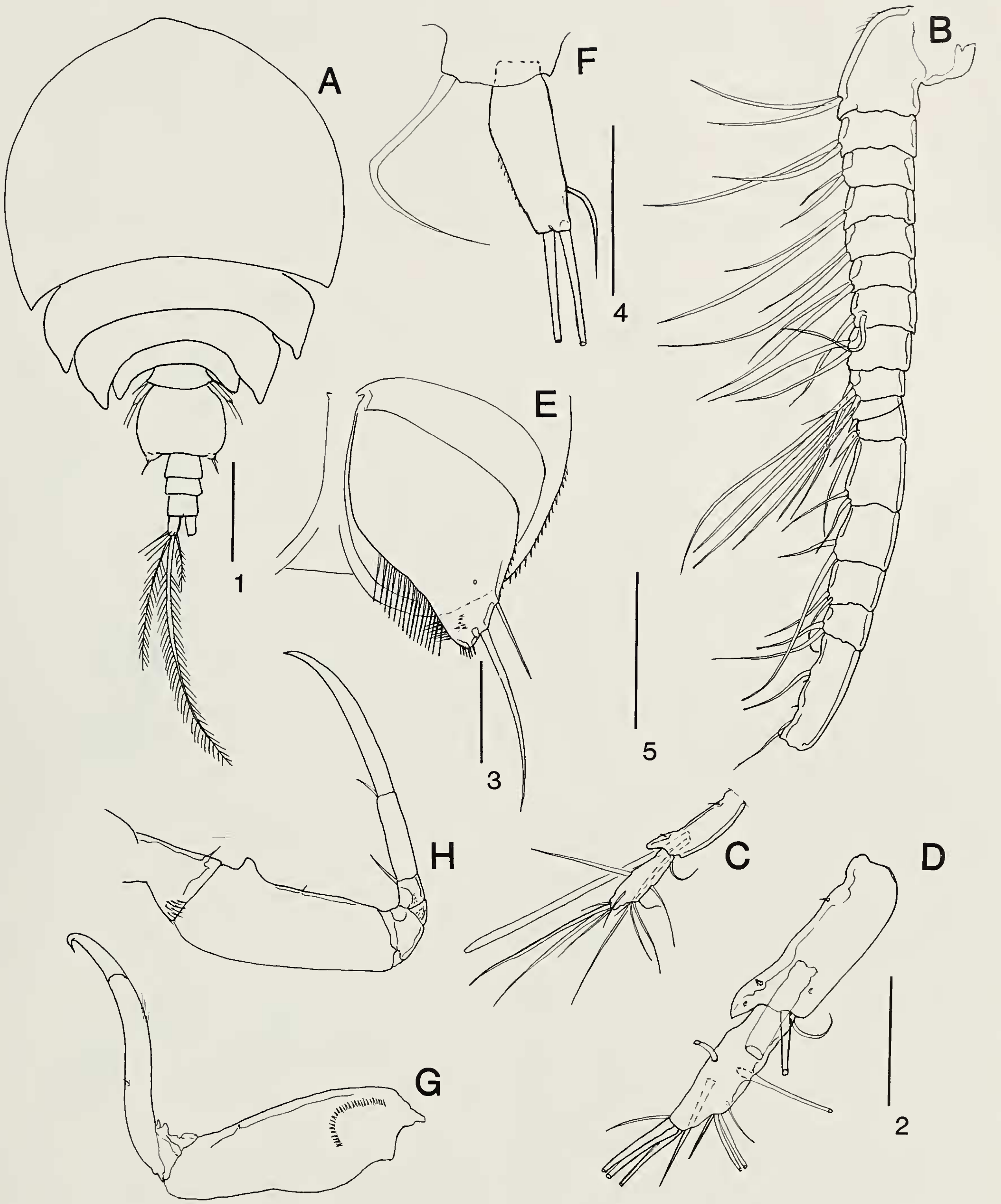

Fig. 12. *Asterocheres lilljeborgi* Boeck, 1859, CVI Male: A, habitus, dorsal; B, antennule, segments 1–16; C, antennule, segments 17–18 anterior; D, antennule, segments 17–18 anterior; E, leg 6; F, leg 5; G, maxilla; H, maxilliped. Scale line 1 is 0.1 mm for A; line 2 is 0.05 mm for D; line 3 is 0.05 mm for E; line 4 is 0.05 mm for B, C, F; line 5 is 0.1 mm for G, H.

mm; length of urosome 0.14 mm; ratio of length to width of prosome 1.2; ratio of length of prosome to length of urosome 2.6.

Urosome (Fig. 15A): Th6, 7, Abd1 articulating.

Antennule (Fig. 15C): 12 articulating segments with 2, 1, 1, 1, 3, 1, 1, 2, 2, 2, 3+1, 14.

Antenna (Fig. 15D), mandible (Fig. 15E) and maxilla (Fig. 15G): As illustrated.

Table 6.—Spines and setae on swimming legs 1–4 of *Asterocheres lilljeborgi* adult female.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0–1	1–1	I-1; I-1; III, I, 3	0–1; 0–2; 1, 2, 3
Leg 2	0–1	1–0	I-1; I-1; III, I, 4	0–1; 0–2; 1, 2, 3
Leg 3	0–1	1–0	I-1; I-1; III, I, 4	0–1; 0–2; 1, 1+I, 3
Leg 4	0–1	1–0	I-1; I-1; III, I, 4	0–1; 0–2; 1, 1+I, 2

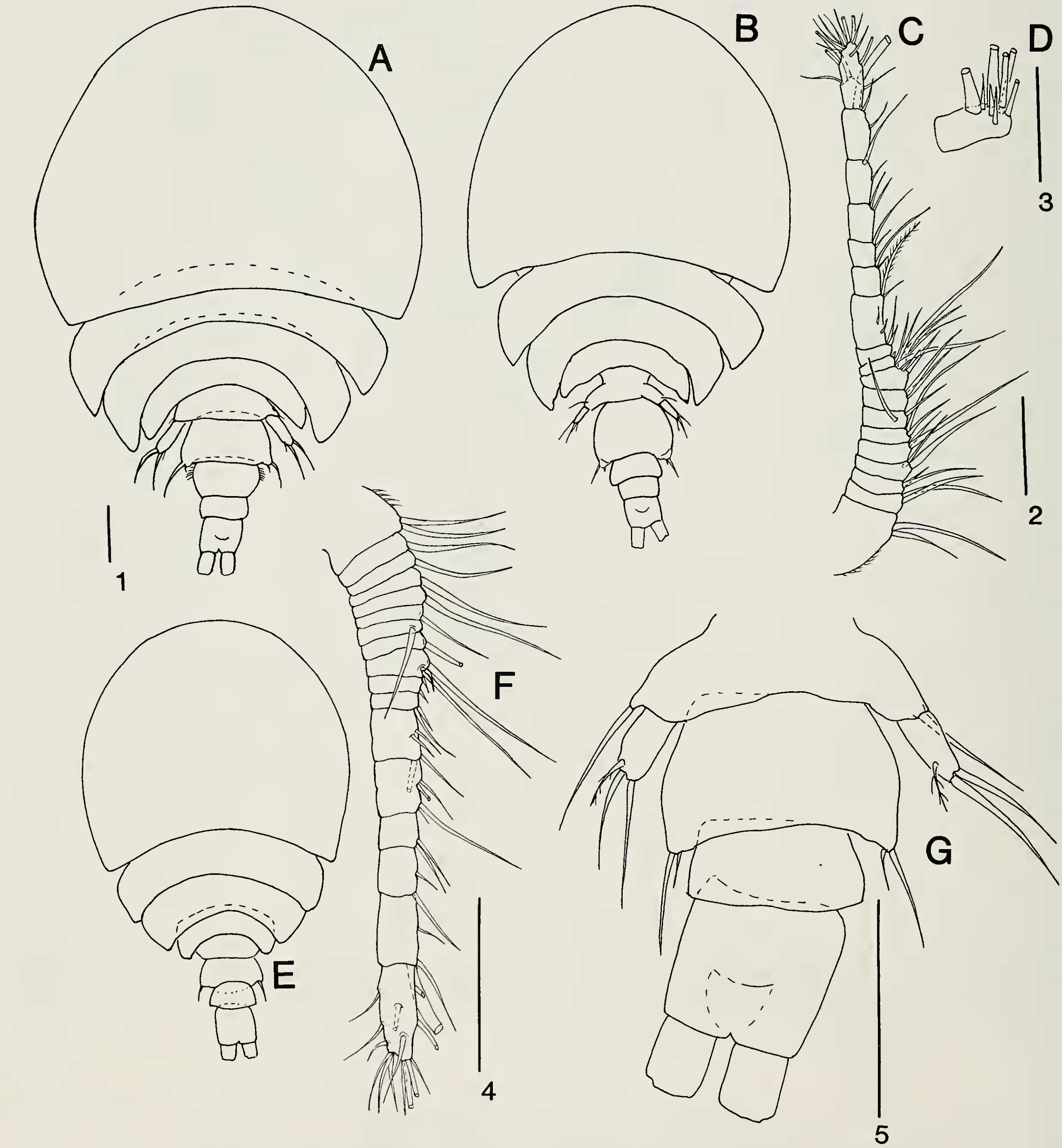

Fig. 13. *Asterocheres lilljeborgi* Boeck, 1859, CV Female: A, habitus, dorsal. *Asterocheres lilljeborgi* CV Male: B, male, habitus, dorsal; C, antennule; D, antennule, segment 9. *Asterocheres lilljeborgi,* CIV: E, habitus, dorsal; F, antennule; G, urosome, ventral. Scale line 1 is 0.1 mm for A, B, E; line 2 is 0.1 mm for C; line 3 is 0.1 mm for D; line 4 is 0.1 mm for F; line 5 is 0.1 mm for G.

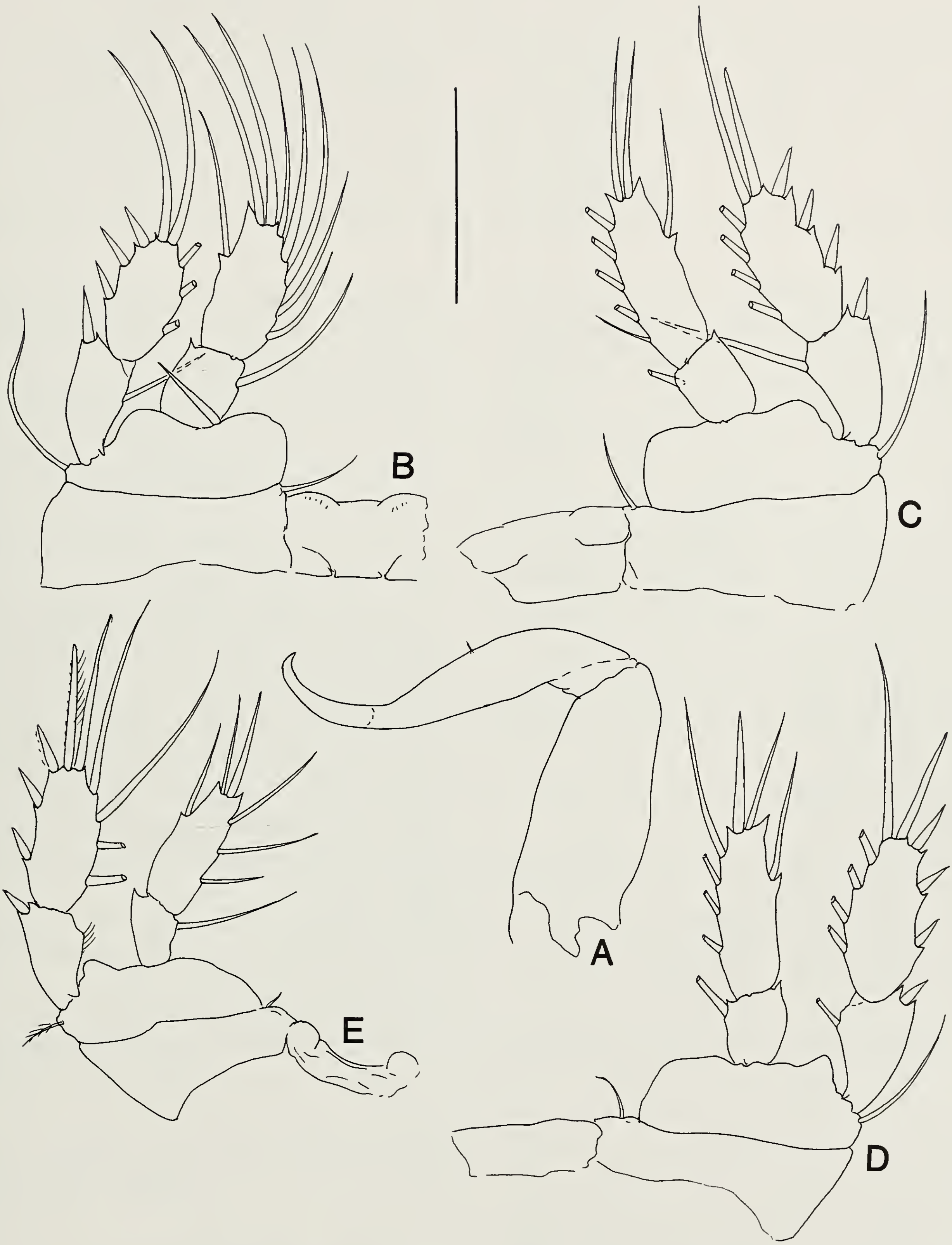

Fig. 14. *Asterocheres lilljeborgi* Boeck, 1859, CIV: A, maxilla; B, swimming leg 1; C, swimming leg 2; D, swimming leg 3; E, swimming leg 4. Scale line is 0.1 mm.

Maxillule (Fig. 15F): Outer lobe with 3 setae.

Maxilliped (Fig. 16A): Proximal section of endopod 3-segmented each with 1 distally polarized seta; distal segment with 2 terminal setae.

Swimming legs 1–4 (Fig. 16B–E): Biramal; swimming legs 1–3 with 2-segmented

Table 7.—Spines and setae on swimming legs 1–4 of *Asterocheres lilljeborgi* CIV female.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0–1	1–1	I-1; *; III, 1, 4	0–1; *; 1, 2, 5
Leg 2	0–1	1–0	I-1; *; III, 1, 5	0–1; *; 1, 2, 5
Leg 3	0–1	1–0	I-1; *; III, I, 5	0–1; *; 1, 1+I, 4
Leg 4	0–1	1–0	I-0; *; III, I, 5	0–1; *; 1, 1+I, 3

rami, swimming leg 4 with 1-segmented rami. Formula for spines and setae (Table 8).

Leg 5 (Fig. 15B): Unilobe bud with 1 distal spine and 1 distal seta.

CII.—Differs from CIII as follows based on 5 specimens: length range 0.41–0.44 mm; average maximum width 0.2–0.22 mm; greatest dorsoventral thickness 0.13–0.14 mm; length of prosome 0.26–0.29 mm, urosome 0.14–0.15 mm; ratio of length to width 2.02:1; ratio of length of prosome to that of urosome 1.95:1.

Prosome (Fig. 17A): 3 articulating sections; 1st a complex of 5 cephalic somites plus Th1, 2; Th3, 4 articulating; Th4 narrow.

Urosome (Fig. 17A): Th5, Th6, Abd1 articulating.

Antennule (Fig. 17C): 9 articulating segments with 2, 1, 2, 1, 1, 1, 1, 1+1, 14.

Antenna (Fig. 17D), mandible (Fig. 17E) and maxilla (Fig. 17F): As illustrated.

Maxillule (Fig. 17H): Inner lobe with 3 setae.

Maxilliped (Fig. 17G): Syncoxa without seta, basis without seta. Endopod 3-segmented; proximal and middle segment each with 1 seta, distal segment with 2 terminal setae.

Swimming legs 1–3 (Fig. 17I–M): Swimming legs 1–2 with 2-segmented rami, swimming leg 3 with 1-segmented rami. Formula for spines and setae (Table 9).

Swimming leg 4 (Fig. 17B): A bilobed bud; dorsal lobe with 1 distal spine and 1 distal setae; ventral lobe unarmed.

CI.—Differs from CII as follows: Body length range 0.38 mm (based on 1 specimen); length of prosome 0.26 mm; maximum width of prosome 0.16 mm; length of urosome 0.12 mm; ratio of length to width of prosome 1.6; ratio of length of prosome to length of urosome 2.2.

Prosome (Fig. 18A): 2 articulating sections; 1st complex of 5 cephalic somites plus Th1, 2; Th3 articulating.

Urosome (Fig. 18B): Th4, 5, Abd1 articulating.

Antennule (Fig. 18C): 4 articulating segments with 2, 2, 1, 14+1.

Antenna (Fig. 18D), mandible (Fig. 18E), maxillule (Fig. 18F) and maxilla (Fig. 18G): As illustrated.

Maxilliped (Fig. 18H): Syncoxa and basis unarmed; endopod 2-segmented; proximal segment with 1 medial seta and distal segment with 1 thick and 1 thin seta.

Swimming legs 1–2 (Fig. 18I, J): 1-segmented rami. Formula for spines and setae (Table 10).

Swimming leg 3 (Fig. 18B): Bilobed bud; dorsal lobe with 1 distal spine and 1 distal seta; ventral lobe unarmed.

CR (Fig. 18B): As illustrated.

Remarks.—Asterocheres lilljeborgi, the type species of the family, can be distinguished from its congeners by exceptionally wide tergites of the dorsoventrally flattened prosome. It has been collected in the Davis Strait, off coasts of the British Isles, Sweden, Norway and France, associated with the starfish *Henricia sanguinolenta* (O. F. Müller, 1776) and other echinoderms (Humes 1986, Gotto 1993). Wilson (1944) found *A. lilljeborgi* associated with *Henricia leviuscula* (Stimpson, 1857) in the Aleutian Islands near Alaska. Marchenkov (1997) reported that *A. lilljeborgi* at the White Sea is associated with *H. sanguinolenta.* Roettger et al. (1972) studied ecology

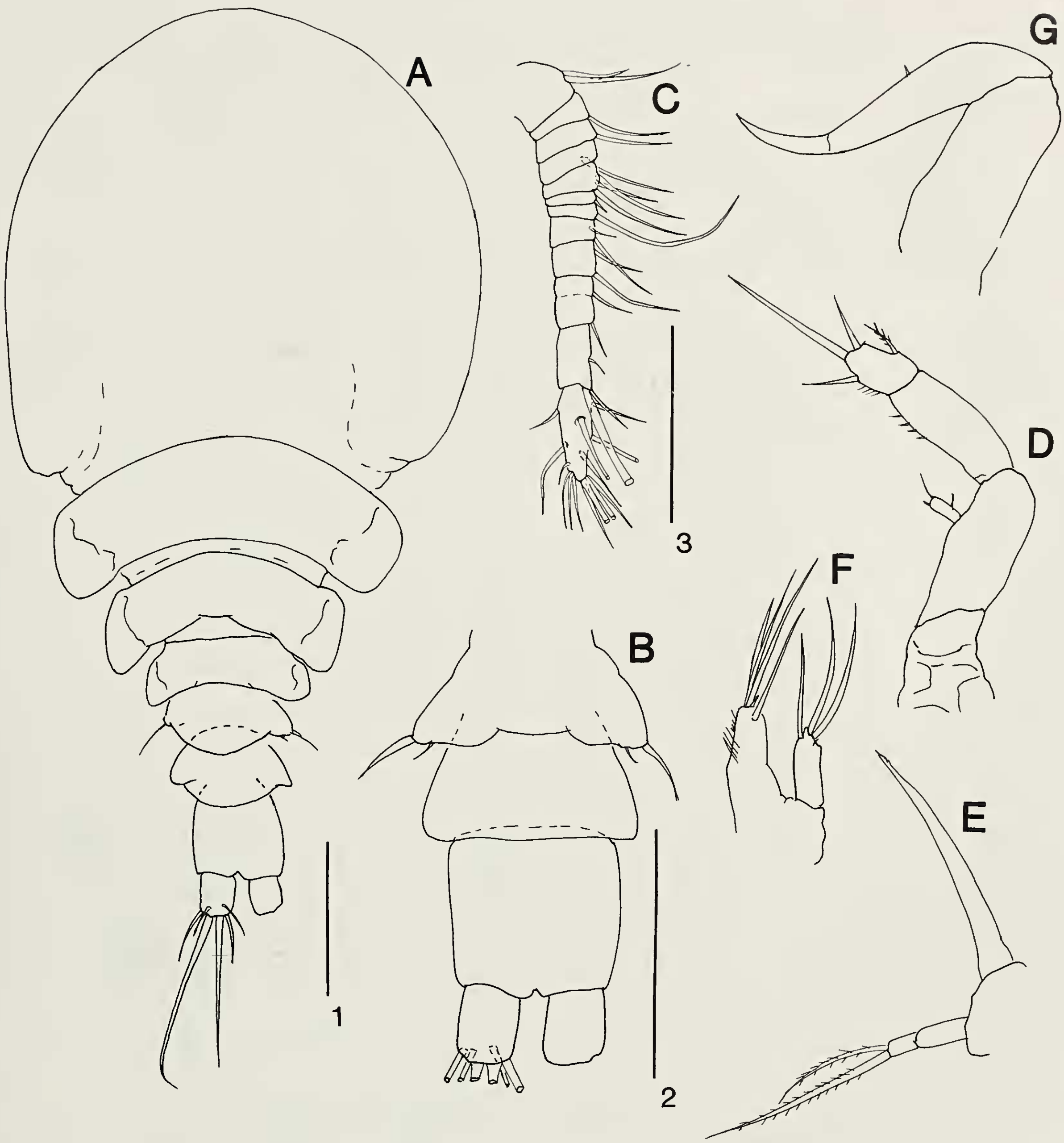

Fig. 15. *Asterocheres lilljeborgi* Boeck, 1859, CIII: A, habitus, dorsal; B, urosome, ventral; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla. Scale line 1 is 0.1 mm for A; line 2 is 0.1 mm for B, D–F; line 3 is 0.1 mm for C.

of *A. lilljeborgi* from *H. sanguinolenta* collected near Sweden.

Discussion

One somite is added to the body of both genders of *Dermatomyzon nigripes* and *Asterocheres lilljeborgi* during the molts to copepodids II–IV, a pattern similar to the related siphonostomatoid *Scottomyzon gibberum* (see Ivanenko et al. 2001). During the molt to copepodid V, both genders of *D. nigripes* add a fourth abdominal somite, but females and males of *A. lilljeborgi* appear to suppress the formation of the fourth somite as do both genders of *S. gibberum*. During the terminal adult molt to CVI, females of *A. lilljeborgi* and *D. nigripes* develop a simple genital complex when an arthrodial membrane separating the genital somite from the second abdominal somite fails to form. This arthrodial membrane does form in females of *S. gibberum* and in males of all three species. The body of the ancestral copepod is assumed to have added

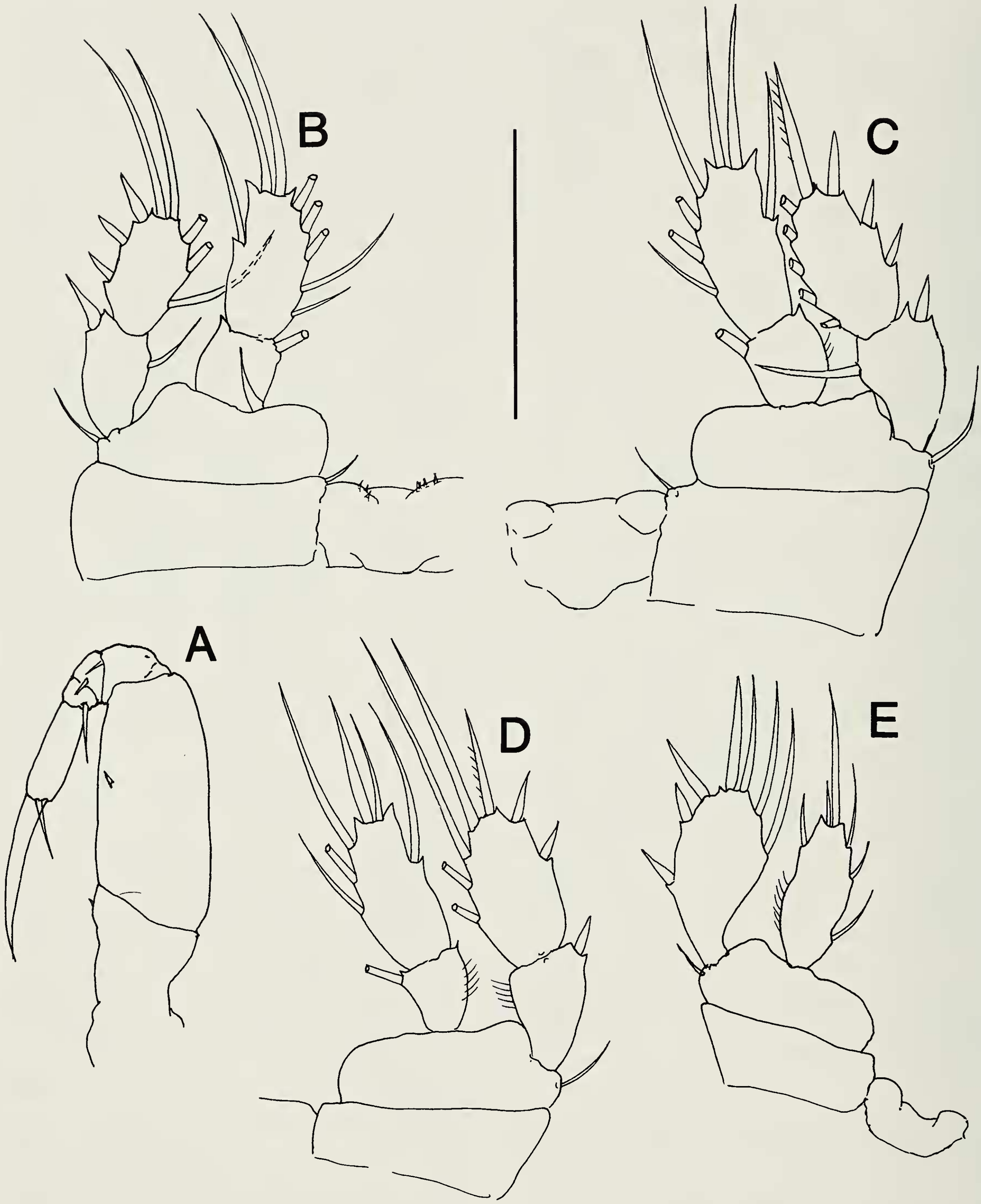

Fig. 16. *Asterocheres lilljeborgi* Boeck, 1859, CIII: A, maxilliped; B, swimming leg 1; C, swimming leg 2; D, swimming leg 3; E, swimming leg 4. Scale line 1 is 0.1 mm.

a somite during the molt of each copepodid stage (Hulsemann 1991), and the arthrodial membrane separating the genital somite from the second abdominal somite remained during the molt to copepodid VI of females, as it does for a few podoplean neocopepods (Martinez Arbizu 2003). The body of the ancestral siphonostomatoid is assumed to have added a somite during the molt of each copepodid stage but the arthrodial membrane separating the female genital somite from the second abdominal

Table 8.—Spines and setae on swimming legs 1–4 of *Asterocheres lilljeborgi* CIII.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0–1	1–1	I-1; *; III, 1, 4	0–1; *; 1, 2, 5
Leg 2	0–1	1–0	I-1; *; III, I, 5	0–1; *; 1, 2, 4
Leg 3	0–1	1–0	I-0; *; II, I, 4	0–1; *; 1, 1+I, 3
Leg 4	0–0	1–0	*; *; III, I, 3	*; *; 1, 1+I, 3

somite failed to form during the molt to copepodid VI. The body of *D. nigripes* appears to be identical to the ancestral siphonostomatoid. The body of *A. lilljeborgi* is derived because the fourth abdominal somite fails to form during the molt to copepodid V of both genders. The body of *S. gibberum* also is derived because a fourth abdominal somite fails to form and because an arthrodial membrane separates the genital somite from the second abdominal somite of females, a character state reversal.

The maxilliped of *D. nigripes* and *A. lilljeborgi,* like *S. gibberum,* begins development at copepodid I with an unarmed syncoxa, an unarmed basis, and a 2-segmented endopod with one seta on the proximal segment and two setae on the distal segment. Both *D. nigripes* and *A. lilljeborgi* add one seta each to the syncoxa and basis at copepodid III. One seta also is added to a distinctly segmented endopod at copepodid II and at copepodid III; a third seta juxtaposed to the proximal seta of the endopod is added at copepodid IV. Patterning of the endopod of the maxilliped of *D. nigripes* and *A. lilljeborgi* during development is assumed to follow the general model for copepods (Ferrari 1995, Ferrari & Dahms 1998, Ferrari & Ivanenko 2001), as it is applicable to siphonostomatoids (Ivanenko et al. 2001). Based on the stage at which each seta is added and its location, the endopod of adult *D. nigripes* and *A. lilljeborgi* is interpreted as 4-segmented. The maxilliped of *S. gibberum* fails to add a seta to its syncoxa during development and the seta on the second, or penultimate, endopodal segment is lost at CIV; both of these states are interpreted as derived.

Swimming leg 1 of copepodid I of *D. nigripes* and *A. lilljeborgi* bears eight exopodal setae and seven endopodal setae, the most common number of elements for these rami at this stage of copepod development (Ferrari 2000). Development from copepodid I is similar for both species with one exception. The proximal medial seta on the third exopodal segment (or the ventral seta on the presumptive fourth segment) of *D. nigripes* fails to form on *A. lilljeborgi* during the molt to CV so that there are three inner setae, not four, on the adult of *A. lilljeborgi.*

Swimming leg 2 of copepodid I of *D. nigripes* and *A. lilljeborgi* bears seven exopodal setae and six endopodal setae, the most common number of elements for these rami at this stage of copepod development (Ferrari 2000). Development from copepodid I is similar for both species with one exception. The proximal medial seta on the third exopodal segment, or ventral seta on the presumptive fourth segment, of *D. nigripes* fails to form on *A. lilljeborgi* during the molt to CV so that there are four medial setae, not five, on the adult of *A. lilljeborgi.*

Swimming leg 3 of copepodid I of both species is a bud with two setal elements on the dorsal lobe, the presumptive exopod, and none on the ventral lobe, the presumptive endopod. The common situation for copepods is three setae on the presumptive exopod and two setae the presumptive endopod (Ferrari 2000). At copepodid II, the transformed limb of *D. nigripes* and *A. lilljeborgi* bears seven exopodal setae and six endopodal setae, the most common number of elements for these rami at this stage of copepod development (Ferrari 2000). De-

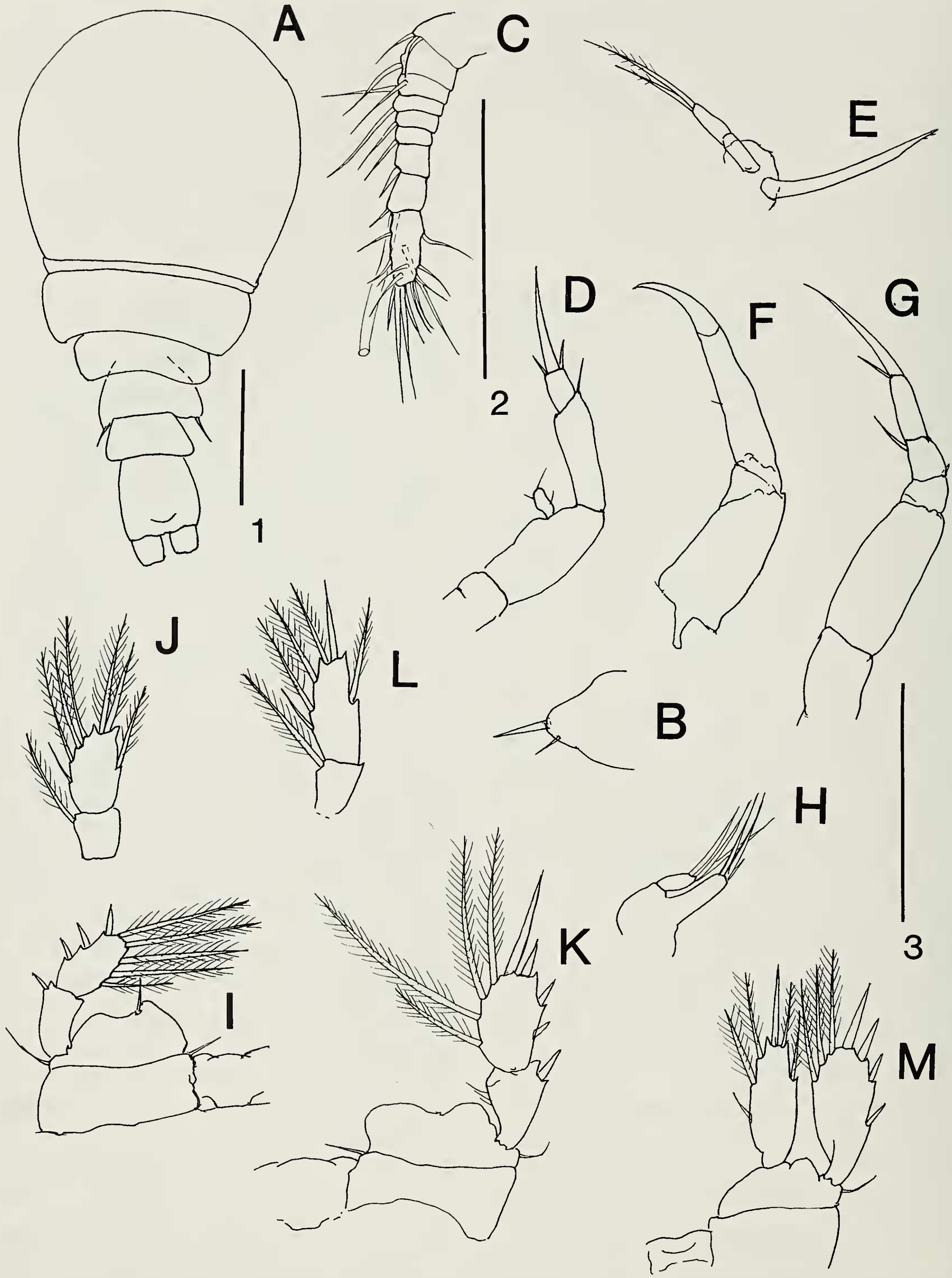

Fig. 17. *Asterocheres lilljeborgi* Boeck, 1859, CII: A, habitus, dorsal; B, swimming leg 4; C, antennule; D, antenna; E, mandible; F, maxilla; G, maxilliped; H, maxillule; I, swimming leg 1, protopod, exopod and intercoxal sclerite; J, endopod of swimming leg 1; K, swimming leg 2, protopod, exopod and intercoxal sclerite; L, endopod of swimming leg 2; M, swimming leg 3. Scale line 1 is 0.1 mm for A; line 2 is 0.1 mm for C; line 3 is 0.1 mm for B, D–M.

Table 9.—Spines and setae on swimming legs 1–3 of *Asterocheres lilljeborgi* CII.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0–1	1–1	I-0; *; III, 1, 4	0–1; *; 1, 2, 4
Leg 2	0–1	1–0	I-0; *; III, I, 4	0–1; *; 1, 1+I, 3
Leg 3	0–0	1–0	*; *; III, I, 3	*; *; 1, 1+I, 3

velopment from copepodid II is similar for both species with two exceptions. *D. nigripes* fails to add a second terminal element to the endopod during the molt to copepodid III, while *A. lilljeborgi* adds this second terminal element. The proximal medial seta on the third exopodal segment, or ventral seta on the presumptive fourth segment, of *D. nigripes* fails to form on *A. lilljeborgi* during the molt to CV so that there are four medial setae, not five, on the adult of *A. lilljeborgi.*

Swimming leg 4 of copepodid II of both species is a bud with two setal elements on the dorsal lobe, the presumptive exopod, and none on the ventral lobe, the presumptive endopod. The common situation for copepods is three setae on the presumptive exopod and two setae the presumptive endopod (Ferrari 2000). At copepodid III, the transformed limb of *D. nigripes* and *A. lilljeborgi* bears seven exopodal setae and six endopodal setae, the most common number of elements for these rami at this stage of copepod development (Ferrari 2000). Development from copepodid III is similar for both species with two exceptions. *D. nigripes* fails to add a second terminal element on the endopod during the molt to copepodid III, while *A. lilljeborgi* adds this second terminal element. The proximal medial seta on the third exopodal segment, or ventral seta on the presumptive fourth segment, of *D. nigripes* fails to form on *A. lilljeborgi* during the molt to CV so that there are four medial setae, not five, on the adult of *A. lilljeborgi.*

Leg 5 of copepodid III of both species is a bud with two setal elements on the dorsal lobe, the presumptive exopod; there is no ventral lobe. At copepodid IV, the transformed limb of both species bears three exopodal setae. At copepodid V of *D. nigripes* a medial and lateral seta are added to the exopod; no setae are added to *A. lilljeborgi.* Leg 6 of copepodid IV of *D. nigripes* is a bud with two setae on the dorsal lobe which is assumed to be the presumptive exopod; a third seta is added during the molt to copepodid V. Leg 6 of copepodid IV of *A. lilljeborgi* is a bud with one seta on the dorsal lobe; a second seta is added to the male during the molt to copepodid V, and to the female during the molt to copepodid VI.

Following the simplifying assumption of oligomerization (Dogiel 1954, Monchenko & Von Vaupel Klein 1999) to infer derived states of swimming legs which develop from serially repeated elements, adults of *S. gibberum* share with those of *D. nigripes* absence of a second terminal element on the third endopodal segment of swimming legs 3–4. Adults of *S. gibberum* share with those of *A. lilljeborgi* absence of the proximal medial seta on the third exopodal segment of swimming legs 1–4, three setae on the exopod of leg 5 and two setae the presumptive exopod of leg 6. Derived states of adult *S. gibberum* include absence of the medial basal seta on leg 1, absence of the medial coxal seta of leg 4, and absence of the proximal lateral seta on the third exopodal segment, or dorsal seta of the presumptive fourth segment, of swimming legs 1–4.

The proximal segment of the antennule of the adult female and male of *A. lilljeborgi* bears two setae. The proximal segment of the antennule of the adult female of *D. nigripes* and *S. gibberum* bears only one seta. One of two setae present on the proximal segment of *D. nigripes* early in

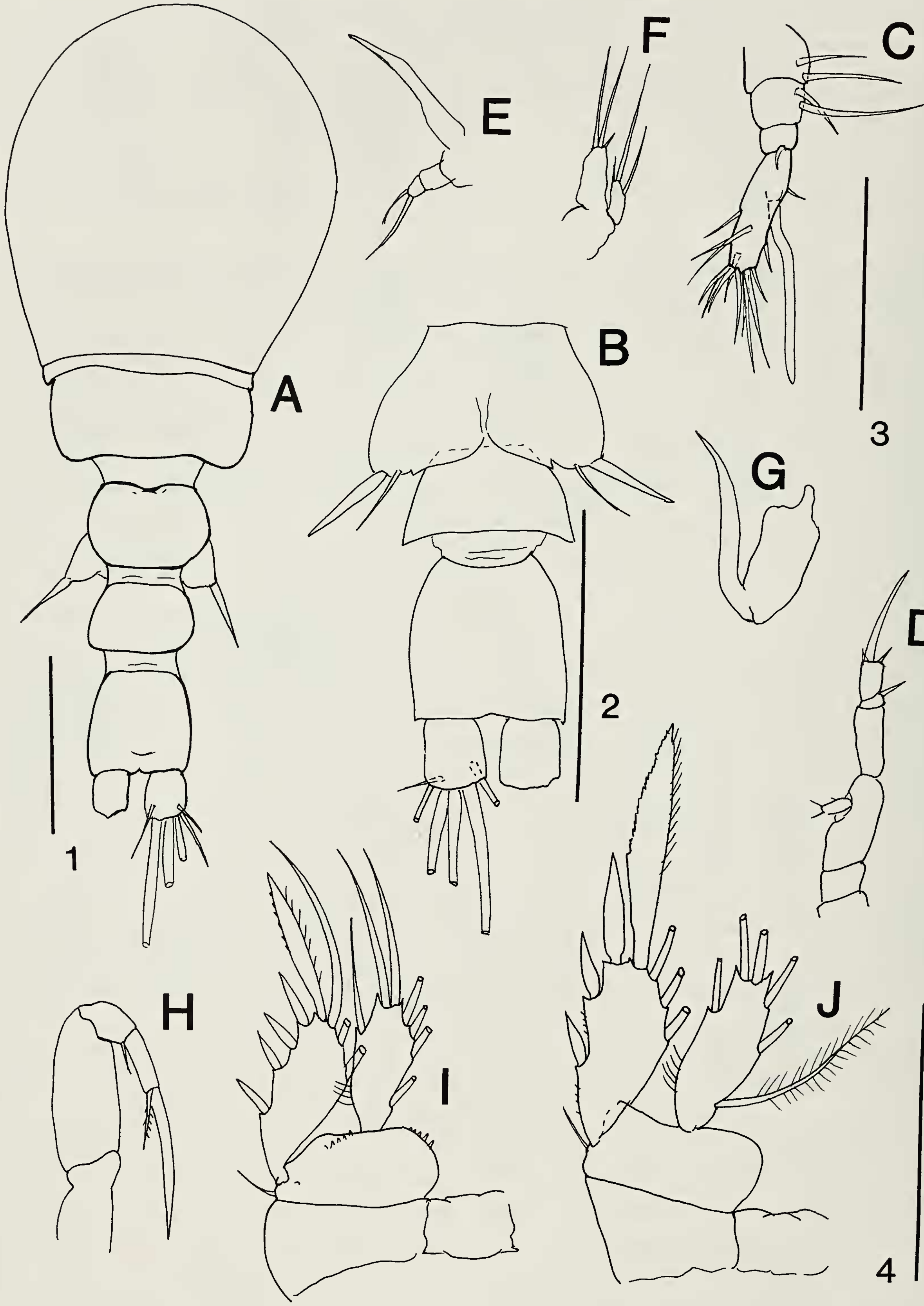

Fig. 18. *Asterocheres lilljeborgi* Boeck, 1859, CI: A, habitus, dorsal; B, urosome, ventral; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, maxilliped; J, swimming leg 1; I, swimming leg 2. Scale line 1 is 0.1 mm for A; line 2 is 0.1 mm for B; line 3 is 0.1 mm for C; line 4 is 0.1 mm for D–I.

Table 10.—Spines and setae on swimming legs 1–2 of *Asterocheres lilljeborgi* CI.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0–0	1–0	*; *; IV, I, 3	*; *; 1, 2, 4
Leg 2	0–0	1–0	*; *; III, I, 3	*; *; 1, 2, 3

development fails to form during the molt to copepodid IV; in contrast the proximal segment of *S. gibberum* bears only one seta throughout the copepodid phase of development.

The ninth articulating segment of the adult female of *D. nigripes* bears only one seta as does the sixth articulating segment of the adult female of *S. gibberum*; these segments are not homologous. The ninth articulating segment of the antennule of the adult female of *A. lilljeborgi* is considered a complex of three segments with six setae, two from each segment. The third articulating segment of the antennule of the adult female of *D. nigripes* is considered a complex of two segments with four setae, two from each segment. The eighth articulating segment of *D. nigripes* is considered a complex of three segments also with six setae, and which corresponds to the complex of *A. lilljeborgi*. The antennule of the adult female of *S. gibberum* also has two complexes, a proximal complex of three segments of six setae and a distal complex of four segments with eight setae. These two complexes correspond to the two of *D. nigripes* but with the following articulating segment of *D. nigripes* fused to the corresponding complex of *S. gibberum*.

The antennule of *A. lilljeborgi* appears to have the fewest derived states: only one segmental complex composed of three proximal segments. The antennule of *D. nigripes* has the following derived states: one seta on the proximal segment; a proximal segmental complex of two segments; and a distal complex of three segments. The antennule of *S. gibberum* has the following derived states: one seta on the proximal segment; a proximal complex of three segments; and a distal complex of four segments.

Acknowledgments

Research of VNI at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. was supported by a Short-Term Visitor Grant from the Smithsonian Institution. Thanks to Dmitry Zhadan and Natasha Cherviakova (Department of Invertebrate Zoology, Moscow State University), and Lena Markhaseva and Alexander Plotkin (Department of Embryology, St. Petersburg State University) for collecting samples. Zbigniew Kabata, Pacific Biological Station, Ju-shey Ho, California State University at Long Beach, and an anonymous reviewer, improved the manuscript immeasurably.

Literature Cited

Boeck, A. 1859. Tvende nye parasitiske Krebsdyr, *Artotrogus orbicularis* og *Asterocheres Liljeborgii*.—Forhandlinger i Videnskabers Selskabet i Kristiania 1859:171–182.

Boxshall, G. A. 1990. Siphonostome copepods associated with sponges from Hong Kong.—Pp. 523–547 *in* B. Morton, ed., The marine flora and fauna of Hong Kong and Southern China, vol. 2. Taxonomy and ecology. Hong Kong University Press, Hong Kong, 449–942.

Brady, G. S. 1880. A monograph of the free and semi-parasitic Copepoda of the British Islands. The Ray Society, London, 3:1–83.

———. 1910. Die marinen Copepoden der deutschen Sudpolar-Expedition 1901–1903. 1. Uber die Copepoden der Stamme Harpacticoida, Cyclopoida, Notodelphyoida und Caligoida.—Deutsche Sudpolar Expedition 1901–1903, 11 (Zoology 3) (5):499–593.

Brady, G. S., & D. Robertson. 1876. Report on dredgings off the coast of Durham and North-Yorkshire in 1874.—Report to the British Association for the Advancement of Science 45:185–199.

Canu, E. 1892. Les Copepodes du Boulonnais. Morphologie, embryologie, taxonomie.—Travaux de l'Institut Zoologique de Lille, Travaux de la Station de Zoologie Maritime de Wimereux 6: 1–292, pls. 1–30.

———. 1893. Un Copepode ascomyzontide sur une algue pelagique.—Notes de biologie marine, fauniques ou ethologiques. I. Annales de la Station Aquicole de Boulogne-sur-Mer 1:100–107, pls. 6–7.

Claus, C. 1889. Ueber neue oder wenig bekannte halbparasitische Copepoden insbesondere der Lichomolgiden- und Ascomyzontiden-Gruppe.—Arbeiten des Zoologischen Institut der Universitat Wien 8:327–370.

Dogiel, V. A. 1954. Oligomerization of the homologous organs as one of the main paths in an animal evolution.—Leningrad University Press, Leningrad [now St. Petersburg], 368 pp.

Eiselt, J. 1965. Revision und Neubeschreibung weiterer siphonostomer Cyclopoiden (Copepoda, Crust.) aus der Antarktis.—Sitzungsberichten der Osterreichischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Abteilung I. 174:51–169.

Ferrari, F. D. 1995. Six copepodid stages of *Ridgewayia klausruetzleri,* a new species of calanoid copepod (Ridgewayiidae) from the barrier reef in Belize, with comments on appendage development.—Proceedings of the Biological Society of Washington 108:180–200.

———. 2000. Patterns of setal numbers conserved during early development of swimming legs of copepods (Crustacea).—Hydrobiologia 417:81–90.

———, & A. Benforado. 1998. Relationships between arthrodial membrane formation and addition of setae to swimming legs 1–4 of *Dioithona oculata, Ridgewayia klausruetzleri, Pleuromamma xiphias,* and *Temora longicornis* (Crustacea: Copepoda).—Crustaceana 71:545–564.

———, & H.-E. Dahms. 1998. Segmental homologies of the maxilliped of some copepods as inferred by comparing setal numbers during copepodid development.—Journal of Crustacean Biology 18:298–307.

———, & V. N. Ivanenko. 2001. Interpreting segment homologies of the maxilliped of cyclopoid copepods by comparing stage-specific changes during development.—Organisms, Diversity and Evolution 1:113–131.

Giesbrecht, W. 1895. The subfamilies, genera, and species of the copepod family Ascomyzontidae, Thorell: diagnosis, synonymy and distribution.—Annals and Magazine of Natural History (6)16:173–186.

———. 1899. Die Asterocheriden des Golfes von Neapel und der angrenzenden Meeres-Abschnitte.—Fauna und Flora des Golfes von Neapel und der Angrenzenden Meeres-Abschnitte, Herausgegeben von der Zoologischen Station zu Neapel 25, 217 pp., pls. 1–11.

Gotto, R. V. 1993. Commensal and parasitic copepods associated with marine invertebrates (and whales): keys and notes for identification of the species.—Synopses of the British Fauna, New Series 46:1–264.

Hansen, H. J. 1923. Crustacea Copepoda. II. Copepoda Parasita and Hemiparasita.—Danish Ingolf-Expedition 3, 92 pp.

Ho, J-s. 1990. A phylogenetic analysis of copepod orders.—Journal of Crustacean Biology 10:528–536. Hulsemann, K. 1991. Tracing homologies in appendages during ontogenetic development of calanoid copepods.—Bulletin of the Plankton Society of Japan, Special Volume, 105–114.

Hulsemann, K. 1991. Tracing homologies in appendages during ontogenetic development of calanoid copepods.—Bulletin of the Plankton Society of Japan, Special Volume, 105–114.

Humes, A. G. 1986. Synopsis of copepods associated with asteroid echinoderms, including new species from the Moluccas.—Journal of Natural History 20:981–1020.

———. 1989. Copepoda from deep-sea hydrothermal vents at the East Pacific Rise.—Bulletin Muséum national d'Histoire naturelle, Paris, 4e série 11, section A. no. 4:829–849.

———. 1999. *Collocherides brychius,* a new species (Copepoda: Siphonostomatoida) from a deep-water hydrothermal site in the northeastern Pacific.—Proceedings of the Biological Society of Washington 112:181–188.

———, & R. U. Gooding. 1964. A method for studying the external anatomy of copepods.—Crustaceana 6:238–240.

Huys, R., & G. A. Boxshall. 1991. Copepod Evolution.—The Ray Society vol. 159, 468 pp.

Ivanenko, V. N., F. D. Ferrari, & A. V. Smurov. 2001. Nauplii and copepodids of *Scottomyzon gibberum* (Copepoda: Siphonostomatoida: Scottomyzontidae, new family), a symbiont of *Asterias rubens* (Asteroidea).—Proceedings of the Biological Society of Washington 114:237–261.

———, & A. V. Smurov. 1997. *Asterocheres flustrae* n. sp. (Copepoda; Siphonostomatoida; Asterocheridae), associated with *Flustra foliacea* L. (Bryozoa) from the White Sea.—Systematic Parasitology 38:111–130.

Jespersen, P. 1940. Non-parasitic Copepoda.—The Zoology of Iceland 3 (33), 116 pp.

Lang, K. 1934. Marine Harpacticiden von der Campbell-Insel und einigen anderen Suedlichen Inseln.—Kunglia Fysiografiska Saellskapets I Lund Handlingar n.f. 45:1–56.

———. 1949. On some Swedish marine semi-parasitic and parasitic copepods.—Arkiv for Zoologi (A) 42(22):1–10.

Linnaeus, C. 1758. Systema Naturae, per regna tria naturae, secundum Classes, Ordines, Genera, Species, cum characteribus, differentiis, synonymis, locis. Ed. decima, reformata. I, Regnum animale: 1–823. Laurentius Salvius, Holmiae.

———. 1767. Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Ed. duodecima, reformata, 1(2):533–1327. Laurentius Salvius, Holmiae.

Marchenkov, A. V. 1997. Fauna of symbiotic and parasitic crustaceans (Copepoda, Isopoda, Cirripedia, Amphipoda) from the benthic invertebrates of the White Sea and Arctic seas.—Parasitologiya 31:24–44.

Martínez Arbizu, P. 2003. The paraphyly of Cyclopinidae Sars, 1913, and the phylogenetic position of poecilostome families within Cyclopoida Sars, 1913 (Copepoda: Crustacea) development.—Organisms, Diversity and Evolution 3 (in press).

Monchenko, V. I., & J. C. von Vaupel Klein. 1999. Oligomerization in Copepoda Cyclopoida as a kind of orthogenetic evolution in the animal kingdom.—Crustaceana 72:241–264.

Mueller, O. F. 1776. Zoologiae Danicae Prodromus, seu Animalium Daniae et Norvegiae indigenarum characteres, nomina et synonyma imprimis popularium. M. Hallager, Havniae, 274 pp.

Nicholls, A. G. 1944. Littoral Copepoda from South Australia. II. Calanoida, Cyclopoida, Notodelphyoida, Monstrilloida and Caligoida.—Records of the Australian Museum 8:1–62.

Pallas, P. S. 1766. Elenchus Zoophytorum, Sistens Generum Adumbrationes Generaliores et Specierum Cognitarum Succinctas Descriptiones, cum Selectis Auctorum Synonymis. Hagae-Comitum, 451 pp.

Roettger, R., H. Astheimer, M. Spindler, & J. Steinborn. 1972. Okologie von *Asterocheres lilljeborgi,* eines auf *Henricia sanguinolenta* parasitisch lebenden Copepoden.—Marine Biology (Berlin) 13:259–266.

Sars, G. O. 1880. Crustacea et Pycnogonida nova in itinere 2do et 3tio expeditionis norvegicae anno 1877 & 78 collecta.—Archiv for Matematik og Naturvidenskab, Christiana 4:427–476 + 60 pls.

———. 1914. Copepoda Cyclopoida. Parts VII & VIII. Cyclopidae (concluded), Ascomyzontidae.—An Account of the Crustacea of Norway, with short descriptions and figures of all the species. Bergen Museum, Bergen 6:81–104, pls. 49–64.

Scott, T. & A. Scott. 1894. On some new and rare Crustacea from Scotland.—Annals and Magazine of Natural History (series 6) 13:137–149.

Sewell, R. B. S. 1949. The littoral and semi-parasitic Cyclopoida, the Monstrilloida and Notodelphyoida.—Scientific Reports of the John Murray Expedition 9:17–199.

Shih, C. T., J. G. Figueira, & E. H. Grainger. 1971. A synopsis of Canadian marine zooplankton.—Bulletin of the Fisheries Research Board of Canada 176:1–264.

Stephensen, K. 1929. Marine parasitic, semiparasitic and non-pelagic Crustacea Copepoda.—The Zoology of the Faroes 2, part 1, section 30:1–18.

Stimpson, W. M. 1857. On the Crustacea and Echinodermata of the Pacific Shores of North America, and is pp. 444–532.—Boston Journal of Natural History 6:444–532.

Stock, J. 1981. Associations of *Hydrocorallia stylasterina* with gall-inhabiting Copepoda Siphonostomatoidea from the south-west Pacific. Part II. On six species belonging to four new genera of the copepod family Asterocheridae.—Bijdragen Tot De Dierkunde 51:287–312.

———. 1984. On the presence of gall-inducing Copepoda on stylasterine corals. Studies on Copepoda II.—Crustaceana supplement 7:377–380.

Thompson, I. C. 1893. Revised report on the Copepoda of Liverpool Bay.—Transactions of the Liverpool Biological Society 7:175–230.

Ummerkutty, A. N. P. 1966. Studies on Indian copepods. 13. Brief notes on the asterocherid copepods obtained from the south east coast of India with description of *Indomyzon qasimi* n. gen., n. sp. and a discussion of the family Asterocheridae.—Crustaceana 11:17–32.

Wilson, C. B. 1944. Parasitic copepods in the United States National Museum.—Proceedings of the United States National Museum 94:529–582.